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**MICROEVOLUTIONARY PATTERNS IN SOME
JURASSIC BIVALVES OF THE OXFORD CLAY,
ENGLAND**

A thesis presented for the degree of Doctor of Philosophy

by

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ABSTRACT

Over 10,000 bivalves were collected to investigate microevolutionary patterns in the Peterborough Member of the Oxford Clay Formation. Two main bivalve lineages were studied *Melagrinella braamburiensis* and *Mesosaccella morrissi*. *M. braamburiensis* was a thin-shelled suspension-feeder and *M. morrissi* was an infaunal deposit-feeder.

These patterns were examined in the context of the new plus ça change model, which has extended the debate on microevolutionary patterns in the fossil record. The model proposes gradualism during narrowly fluctuating, relatively stable environments, and in contrast, net stasis in more unstable environments. The model also predicts for more gradualistic evolution on land in the tropics and in the deep sea, and for more stasis (and occasional punctuations) in shallow waters and temperate zones.

Morphological patterns were detected from two distinctly different sets of environments within the Peterborough Member. The differences in environment were detected through lithological, palaeontological and geochemical evidence. It was found that a more stable period of environmental conditions occurred throughout the majority of the *obductum* Subzone of the Peterborough Member, whilst a period of more fluctuating environmental conditions (in terms of substrate, faunal composition, TOC, OI, carbonate carbon and total sulphur content) prevailed during the *grossouvrei* Subzone of the Peterborough Member.

Bivalves were collected from three localities: Calvert landfill site, Buckinghamshire; Saxon and Orton brick pits, Peterborough. At Calvert and Saxon pits both the more stable environment and the more fluctuating environment, i.e. *obductum* and *grossouvrei* Subzones, were collected from. At Orton pit just the more stable environment, i.e. *obductum* Subzone, was collected from.

Morphological patterns observed for the Length to Height ratio for *M. braamburiensis* showed overall net stasis throughout the more stable environment at Calvert, Orton and Saxon pits, and throughout the more fluctuating environment at Calvert and Saxon pits. The Hinge Length to Anterior Length ratio for *M. braamburiensis* showed positive net morphological change throughout the more stable environment and net stasis throughout the more fluctuating environment at Calvert pit. Net stasis was observed throughout both the more stable and more fluctuating environments at Saxon pit, and was also observed throughout the more stable environment at Orton pit.

Morphological patterns observed for the Length to Height ratio for *M. morrissi* at Calvert and Saxon pits, showed positive net morphological change throughout the more stable environment, with net stasis during the more fluctuating environment. The Hinge Length to Anterior Length ratio for *M. morrissi* showed positive net morphological change during the more stable environment, and net stasis during the more fluctuating environment at Calvert pit. Net stasis was observed throughout both the more stable and more fluctuating environments at Saxon pit. (*M. morrissi* was not studied at Orton pit).

The morphological patterns observed, within the same species, obtained from the two separate geographically areas, are often distinctly different. Local microevolutionary changes or ecophenotypic variation are the two proposed alternatives for this difference.

Overall, the morphological patterns observed from the two bivalve species within the Peterborough Member match, fairly closely, the plus ça change model's predictions for shallow marine invertebrates.

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CHAPTER ONE

INTRODUCTION

1.1 Aims of project

The initial aim of the project was to study the influence of environmental change on detectable microevolutionary patterns from several bivalve species within the Oxford Clay Formation, and specifically within the Peterborough Member (formerly Lower Oxford Clay), which is well exposed across the East Midlands Platform (Figure 1.1).

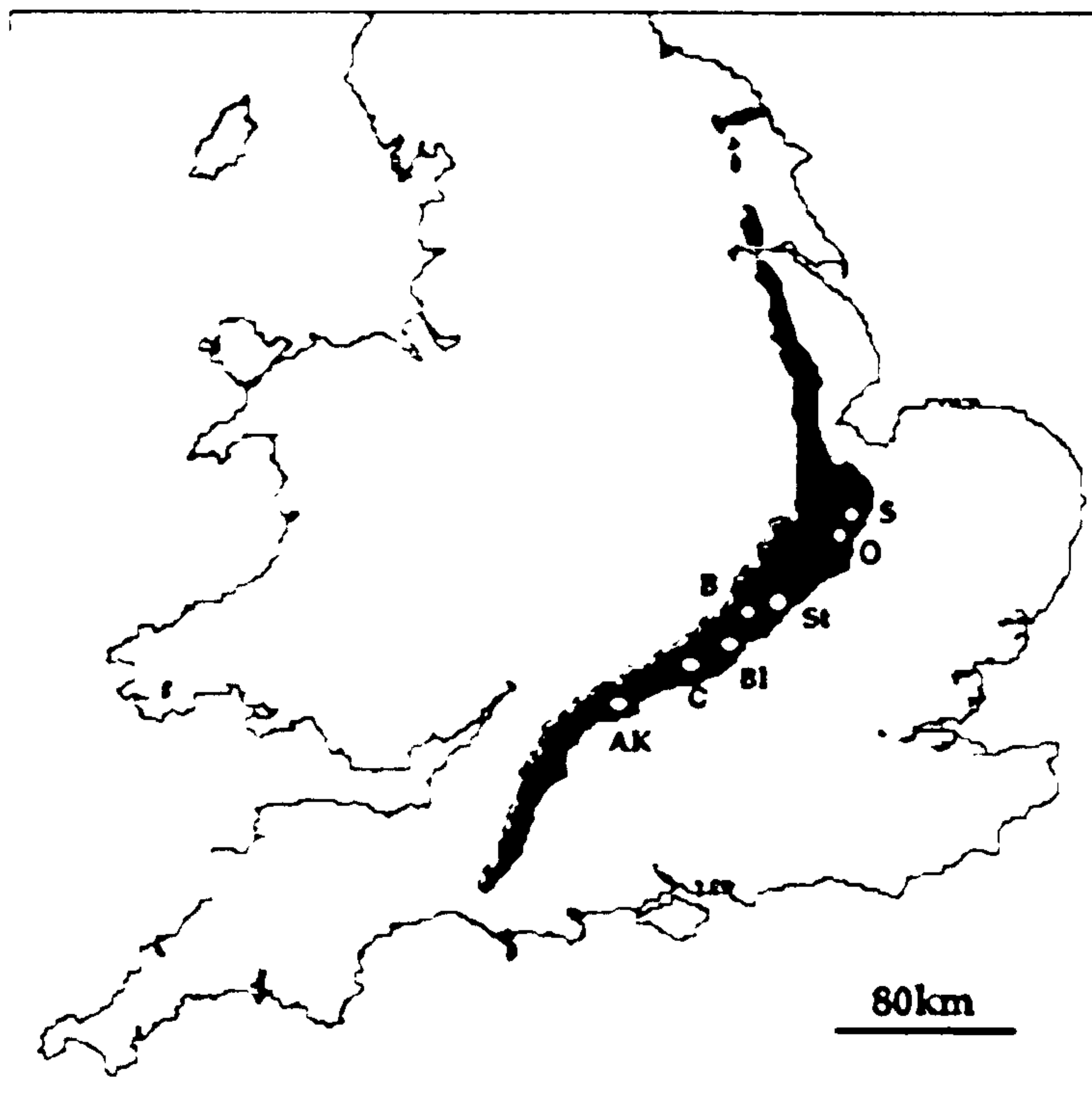


Figure 1.1. Sketch map of the Oxford Clay Formation outcrop of England, after Duff (1978), showing Oxford Clay pit localities: S, Saxon brick pit and O, Orton brick pit, Peterborough; St, Stewartby brick pit and B, Brogborough landfill site, Bedfordshire; Bl, Bletchley landfill site and C, Calvert Landfill site, Buckinghamshire; AK, Ashton Keynes gravel pit, Wiltshire.

Morphological patterns in several bivalve lineages were detected using a high resolution sampling strategy, with populations collected from 200 mm vertical intervals, from the top of the *Kosmoceras jason* Subzone to the base of the *Kosmoceras phaeinum* Subzone (Table 1.1). The morphological patterns were detected from morphometric variation found in the bivalves. Bivalves are abundant, relatively diverse and occur continuously throughout the Peterborough Member (Duff 1978). As high resolution work required adequate numbers of specimens for statistical treatment, thirty specimens of each lineage were collected every 200 mm vertical interval.

1.1.1 Why attempt to detect microevolutionary patterns in the Oxford Clay ?

The Oxford Clay has been studied in considerable detail (see Section 1.2); so why attempt to detect microevolutionary patterns from this formation?

The debate between gradualistic and punctuated modes of evolution continues (Chapter 2), with many patterns emerging from the fossil record from a variety of organisms. Traditionally these patterns have been interpreted as either gradualistic or punctuated modes of evolutionary change. Sheldon (1996b, Figure 2.2a & b) suggested a new evolutionary model for timescales of the order of half a million years or more; plus ça change. Traditional evolutionary theory expects that a changing environment will lead to changing morphology, and that during times of stable environments morphology will remain stable. However, Sheldon (1996a; 1996b) suggested that over relatively long timescales the relationship between the physical environment and phyletic evolution may be the reverse. (The physical environment here includes sea level changes, substrate controls, climatic changes and related factors.) Over geological timescales in more fluctuating environments, the plus ça change model predicts that fauna should be in approximate stasis, maintaining their own kind of stability within wide reflecting boundaries (these boundaries being physical environmental changes such as those listed above). Only when the environment fluctuates outside such boundaries does the fauna respond by evolving rapidly in sudden bursts, and thus achieving a new equilibrium. In quieter, less dynamic environments, with narrowly fluctuating environmental changes, speciation and continuous phyletic evolution are predicted.

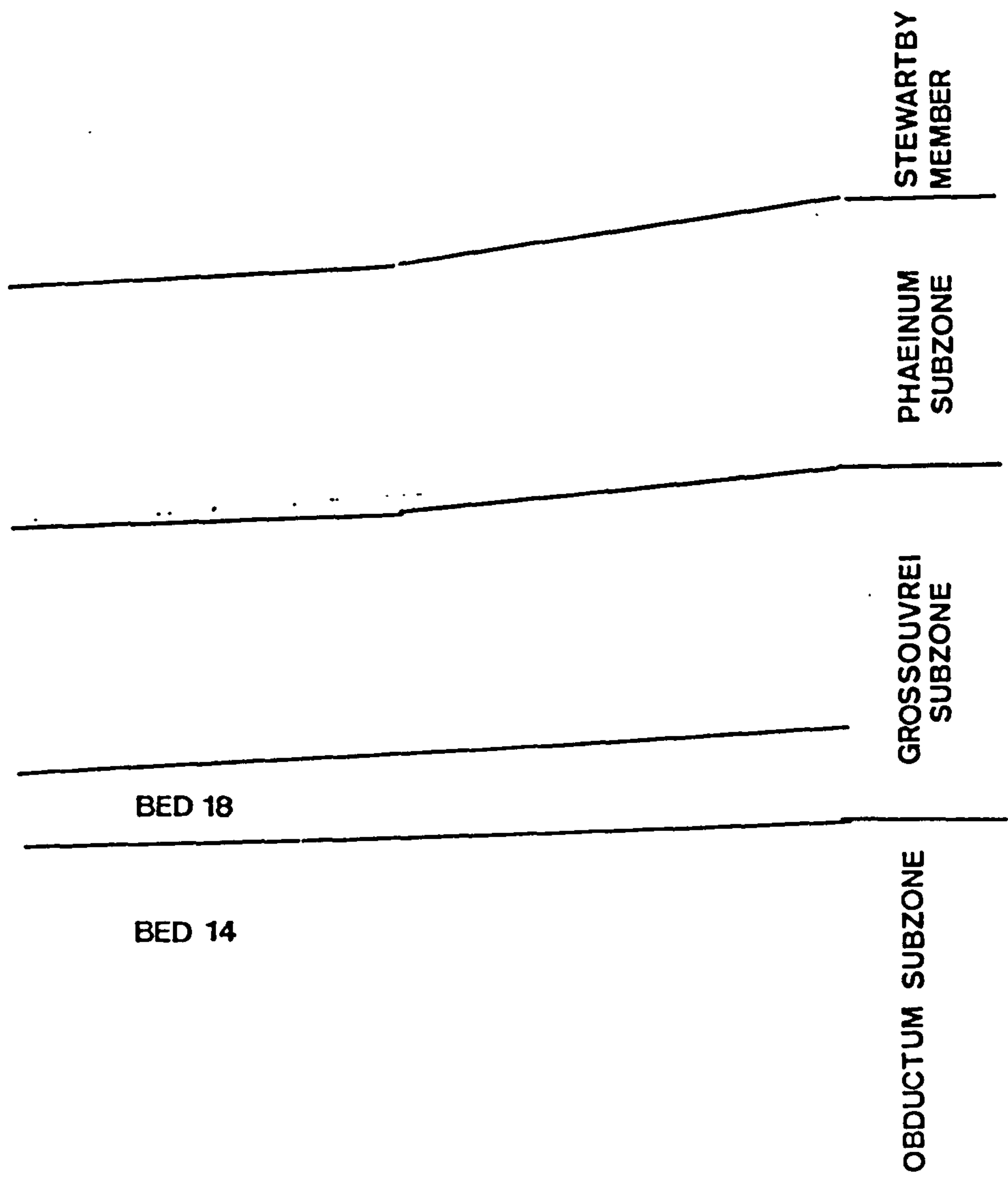
STAGE	ZONE	SUBZONE	STRATA
OXFORDIAN	LOWER	<i>C. cordatum</i>	WEYMOUTH MEMBER
		<i>C. costicardia</i>	
		<i>C. bukowskii</i>	
		<i>C. praecordatum</i>	
		<i>C. scarburgense</i>	
CALLOVIAN	UPPER	<i>Q. lamberti</i>	STEWARTBY MEMBER
		<i>Q. henrici</i>	
		<i>K. spinosum</i>	
		<i>K. proniae</i>	
		<i>K. phaeinum</i>	
	MIDDLE	<i>K. grossouvrei</i>	PETERBOROUGH MEMBER
		<i>K. obductum</i>	
		<i>K. jason</i>	
		<i>K. medea</i>	
		<i>S. enodatum</i>	
	LOWER	<i>S. calloviense</i>	KELLAWAYS FORMATION
		<i>K. galilaei</i>	
		<i>K. curtilobus</i>	
		<i>K. gowerianus</i>	
		<i>M. kamptus</i>	CAYTON CLAY FM
		<i>M. terebratus</i>	ABBOTSBURY CORNBURASH FM
		<i>M. kepleri</i>	(PART)

Table 1.1. Lithostratigraphic subdivision of the Oxford Clay with ammonite zone and subzone nomenclature, after Callomon (1968), Cope *et al.* (1980), Cox *et al.* (1992), Page (1989), and Martill & Hudson (1991).

This study attempts to describe microevolutionary patterns in bivalves from sequences in the Peterborough Member that span both fluctuating environments and relatively stable environments (see Chapter 6), as well as discuss possible models for the results.

The Peterborough Member is ideal for studying these patterns due to its extensive outcrop across the East Midlands, with large fresh exposures in working brickpits and old brickpits used for landfill (Figure 1.1). In addition extensive previous work has been undertaken on the formation i.e., Duff (1975; 1978) and Hudson and his co-workers in the Oxford Clay working group, (e.g. Anderson *et al.* 1994, Belin & Kenig 1994, Hudson & Martill 1994, Kenig *et al.* 1994, Martill *et al.* 1994, Macquaker 1994, Norry *et al.* 1994). These earlier studies have allowed bed by bed analysis to be undertaken, without any problems of identification of the fauna, logging of the sections, and the determination of the biostratigraphy. A relatively stable environment (in terms of lithology, palaeontology and geochemistry) is preserved within the *obductum* Subzone (Figure 1.2, Table 1.1), represented by a great thickness (>4 m) of similar lithology. This is followed in the *grossouvrei* Subzone (Figure 1.2, Table 1.1) by a period where many different lithofacies were deposited, including organic-rich clays, calcareous clays, laminated shales, bituminous shales, and shell beds. These represent a more unstable environment compared to the *obductum* Subzone (see Chapter 6 for full discussion of the environmental changes within the Peterborough Member).

The fauna of the Oxford Clay is very varied, and includes many different types of invertebrates, both nektonic and benthonic, as well as a wide range of vertebrates (Martill *et al.* 1994). To study microevolutionary patterns within a section such as the Peterborough Member, it is desirable to have a continuous lineage throughout the section. This cannot be achieved utilising the vertebrates as they were not sufficiently abundant, and were also in the main highly mobile, therefore could have migrated into the area and hence not be indicative of local environmental changes. Of the numerous invertebrates present, bivalves were selected for study as they are extremely abundant, usually well preserved, have numerous homologous points from which to measure morphometric variables, are continuous throughout the Peterborough Member, and were benthonic.



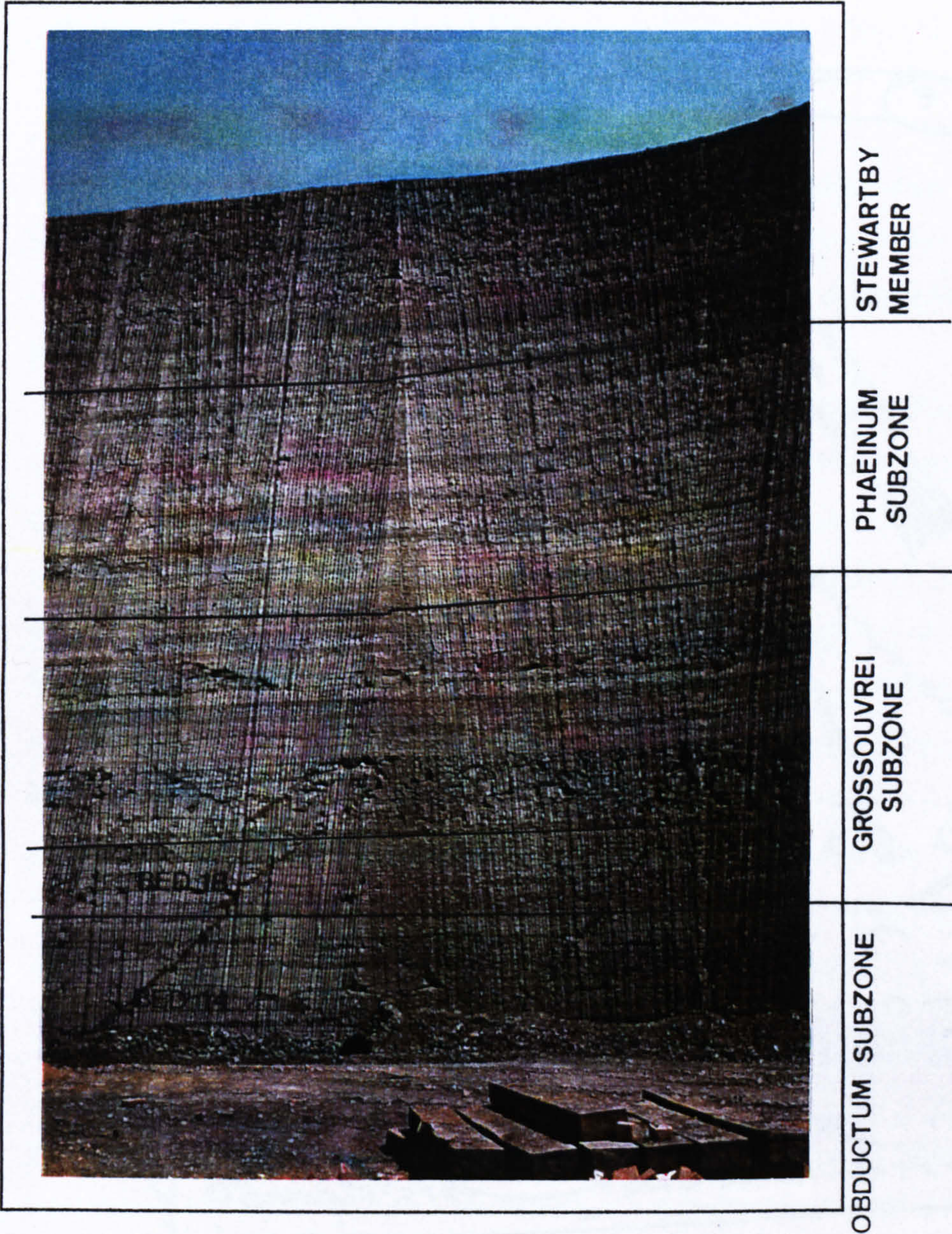
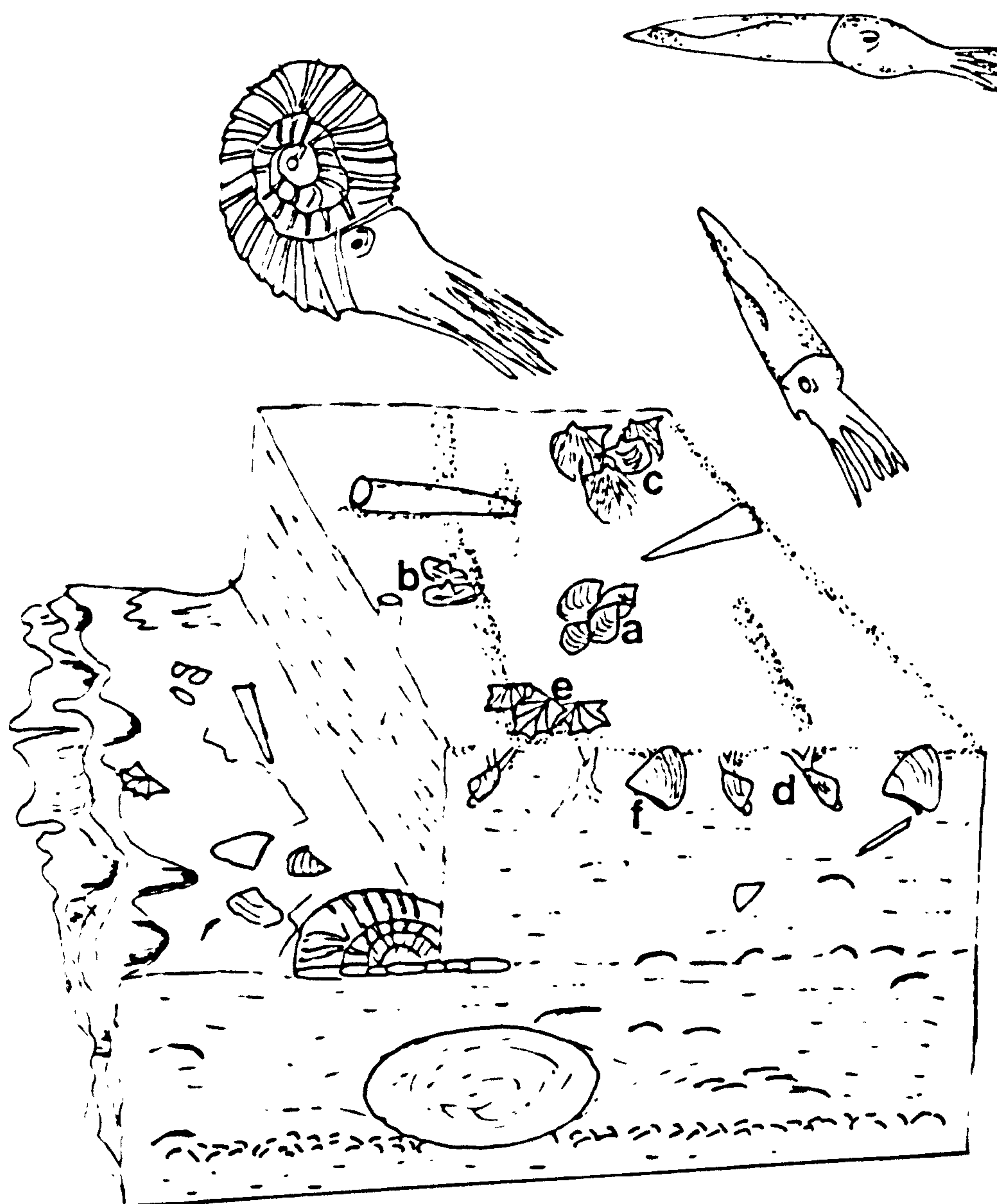


Figure 1.2. Photograph of the working face at Saxon brick pit, Peterborough.

The bivalve fauna of the Oxford Clay can be divided into numerous species/lineages. The six most abundant lineages were selected for this study (Plates 1 & 2): *Bositra buchii* (Roemer 1836), an epifaunal suspension-feeder; *Grammatodon minimus* (Leckenby 1859), an infaunal non-siphonate suspension-feeder; *Meleagrinnella braamburiensis* (Phillips 1829), an epifaunal suspension-feeder; *Mesosaccella morrisi* (Deshayes 1853), an infaunal deposit-feeder; *Oxytoma inequivalve* (Sowerby 1819), an epifaunal suspension-feeder; and *Palaeonucula triangularis* (Duff 1978), an infaunal deposit-feeder (Duff 1978). (Life habitat is shown in Figure 1.3). There are 23 other bivalve species recorded by Duff (1978) in the Oxford Clay, but these were not examined in this study due to their rarity.



- a= *Bositra buchii* (epifaunal suspension-feeder)
- b= *Grammatodon minimus* (infaunal non-siphonate suspension-feeder)
- c= *Meleagrinnella braamburiensis* (epifaunal suspension-feeder)
- d= *Mesosacella morrissi* (infaunal deposit-feeder)
- e= *Oxytoma inequivalve* (epifaunal suspension-feeder)
- f= *Palaeonucula triangularis* (infaunal deposit-feeder)

Figure 1.3. Reconstruction showing the life habitats of the six studied bivalve lineages (modified from Sellwood 1978, pp.210-212). Also shown are ammonites and belemnites.

1.2 A review of the Oxford Clay

1.2.1 History of studies on the Oxford Clay

The Oxford Clay is an extremely important formation due to its commercial value in brick manufacture. Its large fresh exposures make the Oxford Clay an ideal natural laboratory for studying organic matter accumulation, and this has led to extensive study by many workers.

Studies on the Oxford Clay have mainly occurred within the brick pits around the Oxford, Bedford and Peterborough areas. The Oxford Clay lacks good coastal outcrops and therefore the earliest studies such as those of Porter (1861), who described the Oxford Clay merely in terms of its colour and depth, did so from brick pits in the Stanground area of Peterborough (grid reference TL 199 965). Porter obtained more than 50 vertebrae from Stanground, which are now kept in the Sedgwick Museum, Cambridge. Perhaps one of the most remarkable accounts to come from his book is the historical account; unlike present day scientific papers, Porter (1861, pp.61-62) described one of his situations at Stanground in much detail: 'for on riding one day into one of the brick-yards at Stanground, my horse took fright and plunged into a large and tall heap of recently dug clay, and on trying to extricate himself only got deeper into the mire, until both horse and rider were completely stuck fast in the middle; and I shall not readily forget the process employed to release us, for while half-a-dozen men were tugging at my horse with ropes, I was submitted to a somewhat unpleasant process of *unmiring*, which consisted in having buckets of water poured all around my body and legs, until the clay was sufficiently moistened to permit me by a strong system of wriggling to disemtom myself. Had the clay been a little softer, I should have been completely immured, and might perhaps have astonished the *savants* in future generations by so perfect a specimen of a fossil man, booted and breeched. As it was, I returned home, looking more like a clod than a man, and congratulated myself on my escape.'

This is a wonderful account of how palaeontologists practised their trade more than 100 years ago. Today, Porter's account has only historical value.

Phillips (1871) published an early log of the borehole at Wytham, which penetrated the Oxford Clay. Although descriptions of the lithologies are very vague, Phillips provides a full faunal list for the Oxford Clay and, like Porter, emphasises the marine vertebrates.

It was the numerous marine vertebrates that first attracted so many workers to the Oxford Clay Formation, with the main vertebrate collections made

by Charles and Alfred Leeds (see Andrews 1910-13; Leeds 1956 and Martill 1991a, 1991b, pp.192-195).

The Peterborough Member has been exposed in numerous brick pits over the East Midlands during different times. Arkell (1933) described numerous sections exposed in these pits across the whole of the Oxford Clay outcrop, from Dorset to Humberside. Many of these were later re-described by Callomon (1968) who provided full logs of sections from Calvert and Bletchley pits, Buckinghamshire; Stewartby pit, Bedfordshire; and pits around Peterborough.

The stratigraphically higher parts of the Oxford Clay have been studied extensively at Woodham pit, Buckinghamshire by both Arkell (1939) and Hudson & Palframan (1969). Callomon (1968) also provides a stratigraphical log for this pit, and for a pit at Warboys, Cambridgeshire which lies in the Weymouth Member (Upper Oxford Clay).

Probably one of the most important historical studies of the Oxford Clay was by Brinkmann (1929), who used the extensive exposures at Peterborough to carry out a pioneering evolutionary statistical study. The main aim of his work was to record the chronological distribution of the fossil ammonites within the Oxford Clay, looking at species characteristics and their vertical life-span. Brinkmann's study illustrates that successful evolutionary study of macrofauna can be undertaken within the Peterborough Member. His work is discussed in detail in Section 2.6.1

1.2.2 Outcrop

The Oxford Clay outcrops in a thin strip (wider in Lincolnshire) across the country from the North Yorkshire coast at Scarborough, through Lincolnshire and Cambridgeshire, before cutting across the country, through Bedfordshire, and Buckinghamshire to the south coast at Weymouth, Dorset (Figure 1.1). There are also limited exposures of Oxford Clay on the east coast of Scotland (see Arkell 1933, p.365 for details).

Large exposures of the Peterborough Member are now mainly limited to brickpits (operated by Hanson Brick PLC) around the Peterborough and Bedfordshire regions and the new landfill sites (former brick pits, operated by Shanks & McEwan Ltd) in the Peterborough, Bedford and Buckinghamshire areas. Three main pits were studied extensively for this work, with several other pits

examined in less detail. These are described in Chapter 3, and are: Calvert landfill site, Buckinghamshire (grid reference SP 695 232); Saxon brick pit, Peterborough (grid reference TL 248 967); and Orton brick pit, Peterborough (grid reference TL 160 940). The only natural exposures of the Peterborough Member are now seen on the Dorset coast at Tidmour Point near Weymouth.

1.2.3 Stratigraphy

The Oxford Clay Formation spans the Middle/Upper Jurassic boundary, approximately 157-162 Ma. It is an argillaceous formation, with the clay facies declining in importance as sandy deposits dominate in Yorkshire. The Oxford Clay Formation across the East Midlands is a succession of mudrocks with intermittent concretionary carbonate horizons that lies conformably on the Kellaways Formation. It was deposited following the Lower Callovian marine transgression, marking the end of the sandy facies in the Kellaways Formation and the start of the mudstones in the Oxford Clay Formation (Martill & Hudson 1991).

The Oxford Clay has traditionally been split up into three - the Lower, Middle and Upper Oxford Clays. However, the nomenclature has been re-defined by Cox *et al.* (1992), to the Peterborough, Stewartby and Weymouth Members respectively. This project is concerned with the Peterborough Member, which is Upper Lower Callovian to early Upper Callovian in age. The Peterborough Member, being the basal part of the Oxford Clay Formation, rests conformably on the Kellaways Formation over most of its outcrop, (Callomon 1968, Duff, 1978, Martill & Hudson 1991), (Table 1.1). The top of the Peterborough Member is defined as a lithological break between organic-rich shales and more calcareous clays approximately one third of the way up in the *athleta* Zone at the end of the *phaeinum* Subzone (Hudson & Martill 1994, p.119). Although the top of the Peterborough Member is well defined, it is not readily seen. The best place to view the boundary between the Peterborough and Stewartby Members is at the King's Dyke pit, Peterborough (grid reference TL 248 967). Here the brick pit is worked using a 'shale planer' which gives the very shear, clean face illustrating the differences between the two members well (Figure 1.2).

The nomenclature applied to the Oxford Clay by Cox *et al.* (1992) only applies to areas of England south of the Humber, as further north the Middle

Callovian is cut out by an unconformity at the base of the *grossouvrei* Subzone (Duff 1978, Martill & Hudson 1991, Hudson & Martill 1994). The clay facies is only fully developed south of Market Weighton, with a maximum thickness in the Wiltshire region of up to 200 m (Callomon 1968, p.264). Between 130 and 170 m of Oxford Clay is seen at Weymouth (Arkell 1947, p.25), but only 85 m in Cambridgeshire (Callomon, 1968, p.264). There is an overall thinning of the clay towards Market Weighton; the Peterborough Member however, has a relatively constant thickness across the East Midlands of between 16 and 25 m (Figure 1.4).

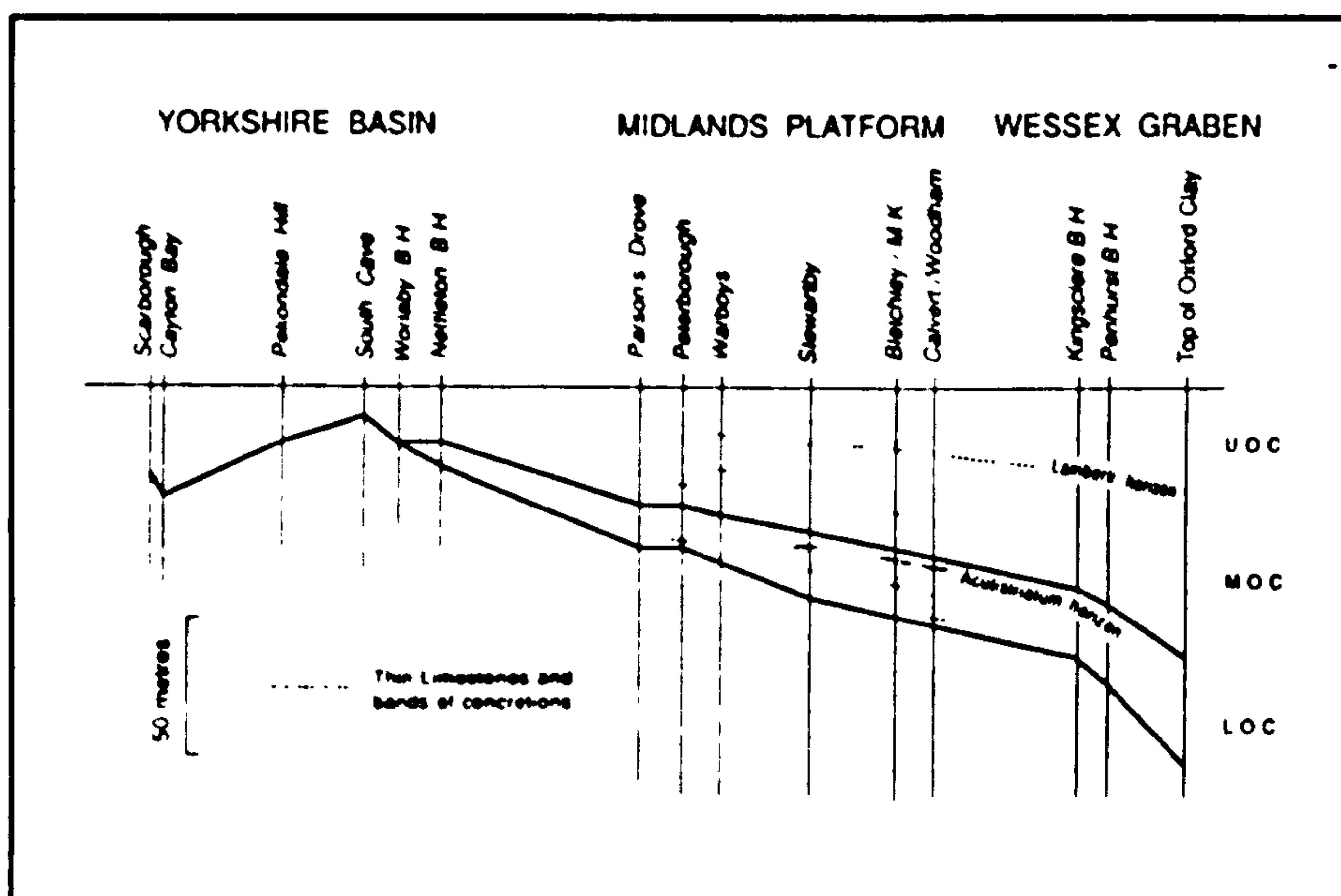


Figure 1.4. To show the variations in thickness of the Oxford Clay in England (LOC, MOC, UOC are Lower, Middle and Upper Oxford Clay respectively, now Peterborough, Stewartby and Weymouth Members); from Martill & Hudson (1991, p.22).

1.2.4 Fauna

The fauna within the Oxford Clay, and more specifically the Peterborough Member, is both diverse and abundant. The ammonites within the Peterborough Member are perhaps the most well known due to the extensive literature that has been published with regards to the ammonite zonal scheme (d'Orbigny 1842-51, Oppel 1856-58, Neaverson 1925, Brinkmann 1929, Arkell 1933; 1939; 1941, Callomon 1955; 1957; 1968; 1969; 1984a; 1984b; 1995, Callomon & Cope 1995, Cope *et al.* 1980, Page 1989; 1991; 1995; 1996). There is also a diversity of other invertebrates and large and small vertebrates. Other molluscs include bivalves, scaphopods, gastropods and belemnites. In addition there are lesser numbers of

annelids, brachiopods, arthropods, foraminifera, microflora, and trace fossils. The invertebrates have been among the least discussed of the fauna within the Peterborough Member, (Sergeant 1961a, Jefferies & Minton 1965, Rood *et al.* 1971, Coleman 1974, Palmer 1975, Riding 1982, Hollingworth 1991); however, Duff (1975) discussed the palaeoecology of the Peterborough Member and monographed the Bivalvia (Duff 1978). The vertebrates of the Oxford Clay have been extensively studied since the end of the last century (see Martill 1991b and references therein). Unfortunately, modern methods of clay extraction (mechanical excavation) mean that few complete specimens are found. More recently Martill & Hudson (1991) summarised the fauna of the Oxford Clay in '*Fossils of the Oxford Clay*'; the faunal list is reproduced in Appendix 1.

1.2.5 Sedimentology

A number of distinct sedimentary and biofacies can be recognised within the Oxford Clay (Hudson & Palframan 1969, Duff 1975). It is predominantly composed of organic-rich mudstones that split readily (shale fissility), revealing the numerous types of fauna (ammonites, bivalves, gastropods etc.). Lithological variations occur throughout the Peterborough Member, distinctly seen from the numerous different types of shell beds and concretionary limestones (Callomon 1968, Duff 1975 and Hudson 1978).

Callomon (1968, pp.277-290) described in detail the Oxford Clay from Peterborough, Bedford, Bletchley, Calvert, Woodham and Warboys pits, in bed-by-bed detail, giving full logs, descriptions of the clays, ammonites and zonal scheme (Callomon 1968, p.265). However, Callomon's account placed an emphasis on the ammonites, due to their leading position in the systematic stratigraphy.

Duff (1974, appendix one, pp.1-35) gave detailed descriptions of stratigraphical sections at four major pits: Calvert, Bletchley, Stewartby, and Peterborough. Note that bed numbers of Duff (1974) do not correlate with those of Callomon (1968); however, the subzonal and zonal boundaries are those defined by Callomon (1968). These descriptions are more recent and were used for this study, however, generally they are not so widely used as Callomon's as they remain unpublished.

More recently Hudson & Martill (1994) selected a type section for the Peterborough Member of the Oxford Clay at the King's Dyke pit near Whittlesey

(grid reference TL 248 967) (Figures 1.1 & 1.2). This is the best and most continuous section currently available in the Peterborough Member, and is close to the section measured by Brinkmann (1929) and Callomon (1968). The pit is worked by a shale planer so the face is steep, and therefore not so convenient for collecting. It is, however, more amenable for measurements (Figure 1.5). The lower beds are characterised by abundant *Gryphaea dilobotes* and Duff (1975) referred to these informally as 'Gryphaea and Reptile Beds'. A further informal marker is bed 18 (Figure 1.5), the 'Dark Bed', which shows up conspicuously in the lower part of the working face (previously called 'black stiff shaly clay' by Brinkmann (1929), and numbered bed 17, 'dark shales', by Callomon (1968)). Two contiguous beds long recognised by their lithology and by ammonites, the Comptoni Bed and the Acutistriatum Bed are important in correlation from Dorset to Humberside (Callomon 1968).

Bed	m	Bed	m
Oxford Clay Formation, Stewarby Member		34	Shale, fissile, burrows at top. <i>Kosmoceras</i> 0 05
6	Mudstone, calcareous, blocky weathering <i>Genicularia</i> , <i>Gryphaea</i> , <i>Procerithium</i> , partially-articulated ichthyosaur (cf. <i>Ophichthosaurus</i>); seen to 2 00	33	<i>Meleagrinitella</i> shell-bed. Much shell hash. Grades into bed above. Nuculaceans 0 06
5	Shale, fissile, weathers white 0 30	32	Clay, blocky, darker than bed below and less fossiliferous 0 30
4	Shale, hard, fissile, prominent bed 0 10	31	Clay, pale greenish grey, more fissile than bed below, nuculaceans 0 20
3	Mudstone, calcareous, hard, blocky; <i>Procerithium</i> , nuculaceans, <i>Meleagrinitella</i> 3 42	30	<i>Meleagrinitella</i> shell-bed. Burrowed, weathers pale Shell-hash, <i>Procerithium</i> , nuculaceans, large <i>Erymnoceras</i> at top 0 22
2	Shale, slightly fissile, pyritized compressed ammonites <i>Meleagrinitella</i> , nuculaceans, <i>Mesoseptella</i> , <i>Procerithium</i> 0 40	29	Clay, greenish. Articulated nuculaceans, <i>Thracia</i> , <i>Meleagrinitella</i> , <i>Genicularia</i> Burrows from base 0 20
1	Mudstone, non-fissile; sharp base 0 50	28	Shale, deposit-feeder shale facies, burrows from bed above filled with green clay Nuculaceans 0 10
Peterborough Member		27	<i>Meleagrinitella</i> shell-bed, much shell hash 0 12
55	Shale, fissile, brown; abundant <i>Meleagrinitella</i> , nuculaceans, <i>Bosire</i> , <i>Dicroloma</i> , <i>Pareunoceramus</i> , fish scale 0 80	26	Shale, deposit-feeder shale facies Nuculaceans 0 08
54	Shell-bed, <i>Meleagrinitella</i> dominant, also nuculaceans 0 10	25	Shell-bed as bed 23 0 02
53	Shale, fissile, brown, fauna as Bed 55, wood associated with <i>Pareunoceramus</i> 0 23	24	Shale, grey-green, weathers dark, burrowed Deposit-feeder shale facies. Much wood, <i>Thracia</i> , coarse-ribbed <i>Kosmoceras</i> 0 68
52	Clay, blocky, green, <i>Meleagrinitella</i> , nuculaceans, shell debris 0 22	23	Shell-bed, rather sparse shells, pyritous Belemnites, wood, <i>Kosmoceras</i> , <i>Hypsocormus</i> tooth, winnowed shell hash 0 01
51	Shell-bed, gradational boundaries, <i>Meleagrinitella</i> dominant, nuculaceans, <i>Procerithium</i> 0 07	22	Shale, less fissile than bed below, gradational base 0 25
50	Shale, shelly, <i>Bosire</i> , <i>Meleagrinitella</i> , <i>Procerithium</i> , <i>Dicroloma</i> , fish scales, wood 0 65	21	Shale, fissile, shelly Abundant nuculaceans Gradational base 0 28
49	Alternations (5–15 cm) of 3 beds of blocky clay and 3 beds of shelly shale with <i>Procerithium</i> etc 0 45	20	Shale, tough, greenish Deposit-feeder shale facies Coprolite Gradational base 0 54
48	Shell-bed, sharp base, gradational top, nuculaceans dominant, <i>Procerithium</i> , <i>Meleagrinitella</i> , <i>Kosmoceras</i> 0 08	19	Shell-bed with clay matrix, pyritic in central 3 cm 0 15
47	Clay, blocky, <i>Meleagrinitella</i> , <i>Procerithium</i> , nuculaceans 0 27	18	Dark Bed Shale, not very fissile, wispy lamination (burrows?) Weathers conspicuously dark grey 1 17
46	Shale, fissile; shell debris and nuculaceans Middle 15 cm less shelly, more blocky 0 67	17	Nuculacean shell-bed, pyritic 0 10
45	Shale, fissile at base passing into hard, blocky, calcareous clay, nuculaceans, <i>Bosire</i> , <i>Procerithium</i> , <i>Kosmoceras</i> , <i>Belemnites</i> , burrows 0 34	16	Shale as bed 14 0 20
44	Clay, bluish, calcareous, gradational boundaries 0 15	15	Shale, fissile, white-weathering, 2 cm nuculacean shell-bed at top 0 16
43	Shale, less fissile than bed below, shelly, gradational base 0 30	14	Shale, not very fissile, rather inconspicuous large burrows, not very fossiliferous and rather homogeneous. Deposit-feeder shale facies Sporadic calcareous and pyritic septarian concretions up to 30 cm diameter with well-preserved juvenile <i>Meleagrinitella</i> , 1.5 m below top 3 80
42	Shale, fissile, brown, pyritized shell hash <i>Kosmoceras</i> , <i>Hecaticeras</i> , nuculaceans, fish scales 0 67	Beds 1–13, 'Gryphaea and Reptile Beds'	
41	Clay, greenish, becoming bluish upwards Nuculaceans, articulated and disarticulated in all orientations, <i>Procerithium</i> , <i>Dicroloma</i> 0 35	13	Shell-bed, rounded clasts of wood 0 02
40	Shale, slightly fissile becoming more so upwards, brown Deposit-feeder shale facies, <i>Procerithium</i> , <i>Kosmoceras</i> fragments, shell hash Top of bed slightly burrowed 0 36	12	Shale, organic-rich, fissile in lower part, ammonites 0 46
39	Clay, greenish Large perisphinctids form shell-layer at base <i>Kosmoceras</i> , <i>Genicularia</i> , coprolites 0 10	11	Shell-bed <i>Gryphaea</i> , <i>Grammatodon</i> 0 04
38	Arcturium Bed. Shale, brownish, fissile especially towards top Large burrows at top with fill of greenish clay, also <i>Chondrites</i> <i>Kosmoceras phaeum</i> microconchs [<i>K. aculeatum</i>] abundant coarse-ribbed <i>Kosmoceras</i> , nuculaceans, <i>Pareunoceramus</i> , perisphinctids 0 33	10	Shale, fissile, organic-rich, burrows in upper part, large calcareous septarian concretions. Ammonites abundant 0 17
37	Comptoni Bed. Nuculacean shell-bed, gradational base <i>Binausphinctes</i> , <i>Cylindroceratulus</i> , <i>Procerithium</i> 0 12	9	Shell-bed, pyritous <i>Gryphaea</i> 0 01
36	Shale, brownish, becoming less shelly upwards Deposit-feeder shale facies <i>Erymnoceras</i> near base 0 56	8	Shale, fissile, dark, organic-rich Ammonites abundant, <i>Gryphaea</i> 0 09
35	Nuculacean shell-bed, sharp base, becomes gradationally less shelly upwards <i>Meleagrinitella</i> , <i>Procerithium</i> 0 09	7	Shell-bed, pyritous at top <i>Gryphaea</i> , <i>Pinna</i> , <i>Kosmoceras</i> 0 05
		6	Shale, fissile, grey, abundant <i>Kosmoceras</i> , <i>Meleagrinitella</i> , <i>Pinna</i> , spat 0 14
		5	<i>Gryphaea</i> shell-bed <i>Gryphaea</i> shells in life orientation and inverted, belemnites, ammonites, wood 0 03
		4	Shaly clay, brown <i>Gryphaea</i> inverted 0 03
		3	<i>Gryphaea</i> shell-bed, pyritous <i>Gryphaea</i> inverted, belemnites 0 04
		2	Shaly clay, olive-brown Transitional base 0 06
		1	Clay, silty Sharp base 0 06

Figure 1.5. Log of King's Dyke pit, Whittlesey, from Hudson & Martill (1994).

Hudson and Martill (1994) re-numbered the section of Peterborough Member and Stewartby Member, starting at the base of the Peterborough Member, defined as above the last silty sand of the Kellaways Formation (as defined by Callomon 1968, Cox *et al.* 1992). The bed numbers of Hudson & Martill coincide with Callomon (1968) and Duff (1978) from bed 8 to bed 14. The Duff and Callomon sections diverge at about bed 15; Duff (1974) employs a more detailed subdivision up to and including the *Acutistriatum* Bed. Hudson & Martill's bed numbering is similar but not identical to Duff's Peterborough section. Hudson & Martill's section at Whittlesey continues above Duff's (1975) section into the Stewartby Member.

The main Peterborough Member facies are described in Chapter 4, although the lithologies as a whole can be split into four broad types: clay-rich mudstones, silt-rich mudstones, shell beds and concretionary limestones.

Clay and silt-rich mudstones: These comprise most of the bituminous shale facies of Duff (1975) and are the largest proportion of the Peterborough Member.

Shell beds: Numerous different types of shell bed were recognised by Callomon (1968), Duff (1974; 1975 and 1978) and Hudson & Martill (1994). Two main types of shell bed were encountered within this study: nuculacean shell beds, and *Meleagrinnella* shell beds. Both are discussed more fully in Section 4.2.2.

Concretionary limestones: Concretionary limestones form mainly as septarian concretions and nodules of predominantly calcite (Hudson 1978, p.340). Most of the concretions found within the Oxford Clay come from the Peterborough Member and occur as two types: main concretions and *Acutistriatum* concretions. The 'main' concretions occur throughout the Peterborough Member uncrushed, or partly crushed often containing fossils, with septarian cracks (these cracks and their infillings are not regular and the infillings may be brecciated). Pyrite is conspicuous in some of them and they started to form before compaction of the sediment (Hudson 1978, p.341), e.g. bed 6 near the top of the *obductum* Subzone at Calvert pit (Duff 1974), and bed 10 at Peterborough (Callomon 1968, Duff 1974, Hudson & Martill 1994). *Acutistriatum* concretions occur at or near the *Acutistriatum* Bed (Duff 1975), at the boundary between the Peterborough Member and Stewartby Member. These are less pyritic and less densely cracked than the main concretions, and they contain flattened ammonites; therefore

concretion growth post-dates some compaction (Hudson 1978, p.341), e.g. the *Acutistriatum* Bed at Calvert pit (bed 12, Duff 1974, or bed 10, Callomon 1968).

1.2.6 Biostratigraphy and correlation

The original correlation of the Peterborough Member throughout the East Midlands, particularly regarding the groups of brick pits around Stewartby, Bedfordshire, and Bletchley and Calvert, Buckinghamshire, was established by Callomon (1968). Refinements were made by Horton *et al.* (1974), Duff (1975, 1978), and Page (pers. comm. 1996). Correlation away from the Peterborough area is based largely on the ammonites. Individual lithologically-defined beds, with the exception of the Comptoni and *Acutistriatum* Beds, have not been generally used to correlate between localities. However, during this study it has been proposed that other lithologically distinct beds may be correlated across the region from Calvert Pit, Buckinghamshire to the Peterborough area (see Section 3.5.2).

It was only quite recently that a subzonal scheme was established for the Stewartby Member of the Oxford Clay by Callomon and Sykes in Cope *et al.* (1980, pp.46–48).

More recently, Page (1989; 1991; 1995; 1996) has revised the stratigraphical divisions within the Lower Callovian and reassessed the ammonite zonation. Page (pers. comm. 1996) provides one of the most comprehensive summaries of all zones and subzones of the Oxford Clay (see Section 3.5.1.3 for details).

1.2.7 Palaeoecology

The most important analysis of the palaeoecology of the Peterborough Member is by Duff (1975). He recognised ten biofacies within the Peterborough Member, subdivided by faunal content and lithology:

- silts and silty clays
- deposit-feeder bituminous shales
- *Grammatodon*-rich bituminous shales
- foraminifera-rich bituminous shales
- nukulacean shell beds,
- *Grammatodon*-rich shell beds

- *Gryphaea* shell beds
- *Meleagrinella* shell beds
- blocky clays
- calcareous clays

(see Section 4.2 for detailed descriptions). Duff agreed with Hallam (1967) that the bituminous shales were deposited in relatively shallow, calm, but not stagnant water, below wave base. The evidence for this is represented, in part, in the deepening sequence from the Kellaways Formation into the Peterborough Member. The many small scale lithological variations seen by Duff (1975, pp.451-452) within the Peterborough Member indicate relatively shallow-water deposition, where a slight change in water depth could have a marked effect on hydrographic conditions.

Duff (1975, pp.461-462) discussed the relationships between the biofacies and this is utilised in Section 4.4, where the environments of deposition are discussed.

The organic carbon content of the Oxford Clay was found to be variable; between 4 and 10% (Fisher & Hudson 1987) and the sediment thought to be deposited under dysoxic conditions (Kenig *et al.* 1994). Martill *et al.* (1994, p.174) therefore suggesting that the sea floor might not have been suitable for burrowers, and only suitable for organisms that 'swam' through the pelletal sediment, or floated within it. Thin pavements of *M. braamburiensis* occur throughout the Peterborough Member (see Section 4.4) (Duff 1975). Martill *et al.* (1994) believed these to be colonisation events, but only after winnowing revealed firmer substrates. Further examination of the sediments within this study revealed that these thin pavements rarely contain other bivalve fauna, such as the shallow infaunal *M. morrisi*.

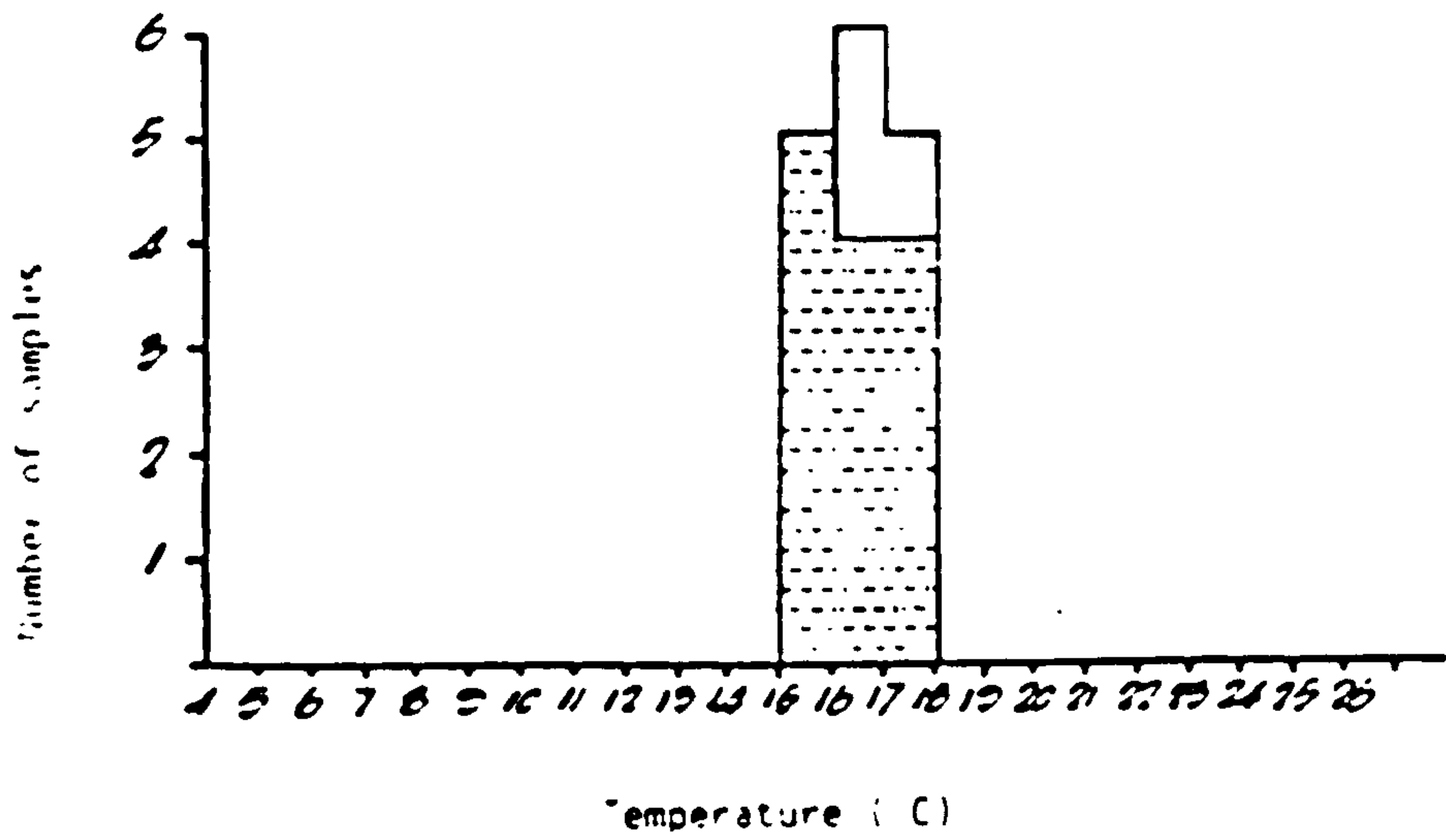
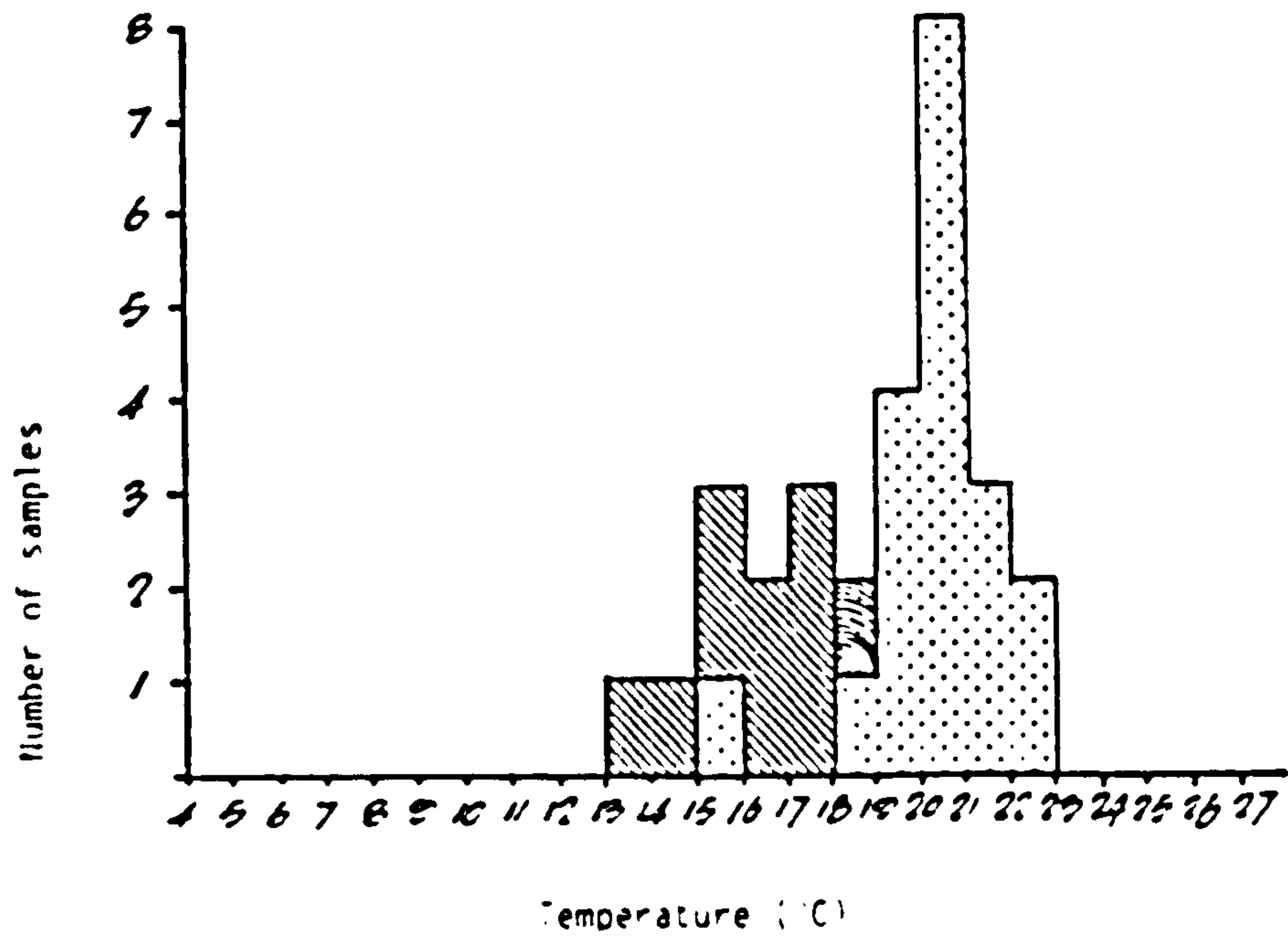
The taphonomy of the Oxford Clay shell beds has been shown to be complex and further study is needed; this has been partly undertaken here and is reported in Section 6.2.2.

1.2.8 Palaeoenvironmental and stable isotope studies.

Palaeotemperatures for the sea waters were discussed by Williams (1988, pp.90), who interpreted the palaeoenvironmental temperature variations through stable isotope work and interpreted anomalously high $\delta^{13}\text{C}$ values for the benthic bivalves within the Peterborough Member.

Williams (1988) studied the palaeotemperatures of individual fossils from the Peterborough Member, and found that *Kosmoceras* precipitated their shells in waters of 17-23 °C; *Gryphaea* precipitated their shells in waters at temperatures of between 11-18 °C; whereas belemnite palaeotemperatures were found to be around the same temperature range as those derived from *Gryphaea*.

Williams (1988, pp.96-99) serially-sectioned a belemnite guard to study its palaeotemperatures and found temperatures ranging from 12-19.7 °C. However, *Meleagrinella* was found to precipitate its shell at the same temperatures as *Gryphaea* (Figure 1.6a & b).








- | | | | |
|---|-----------------|---|-------------|
|  | Mesmoceras |  | Grypnaea |
|  | Cnoffaria |  | Meleagrinea |
|  | Cylindroteuthis | | |

Figure 1.6a. Temperature histogram for μson Zone Peterborough, from Williams (1988, p.89).

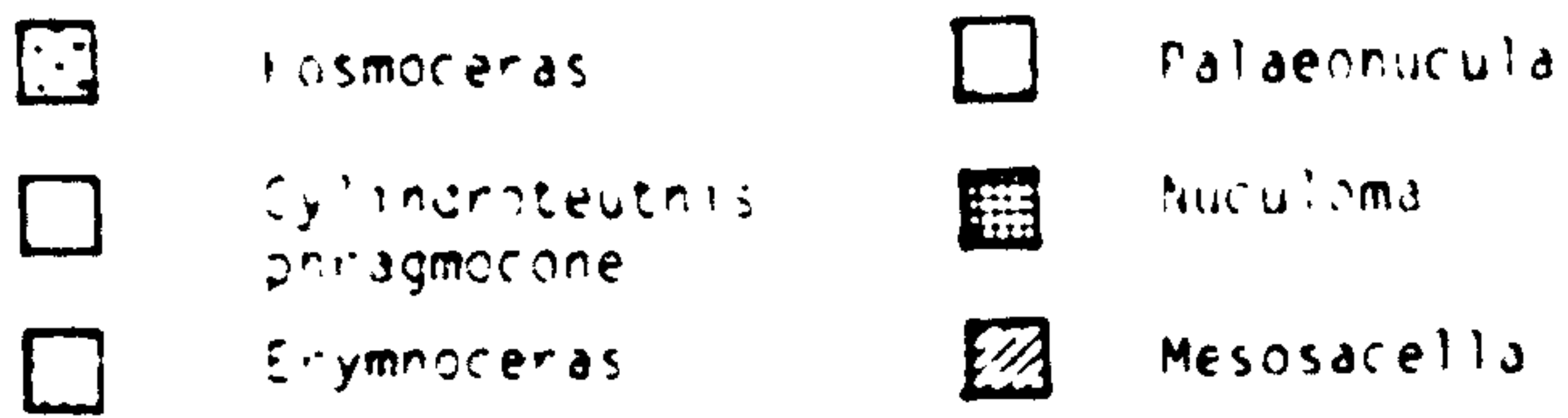
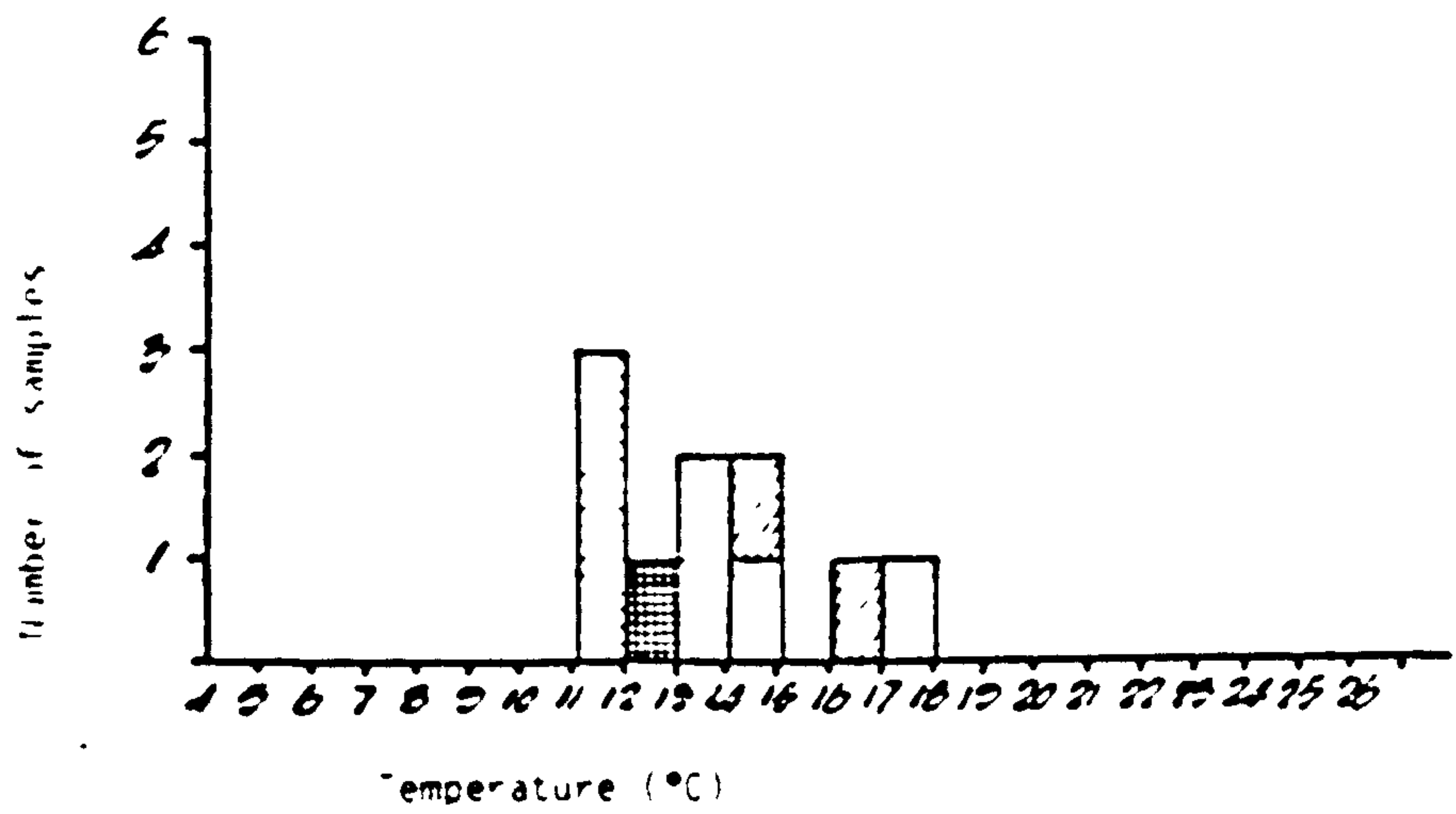
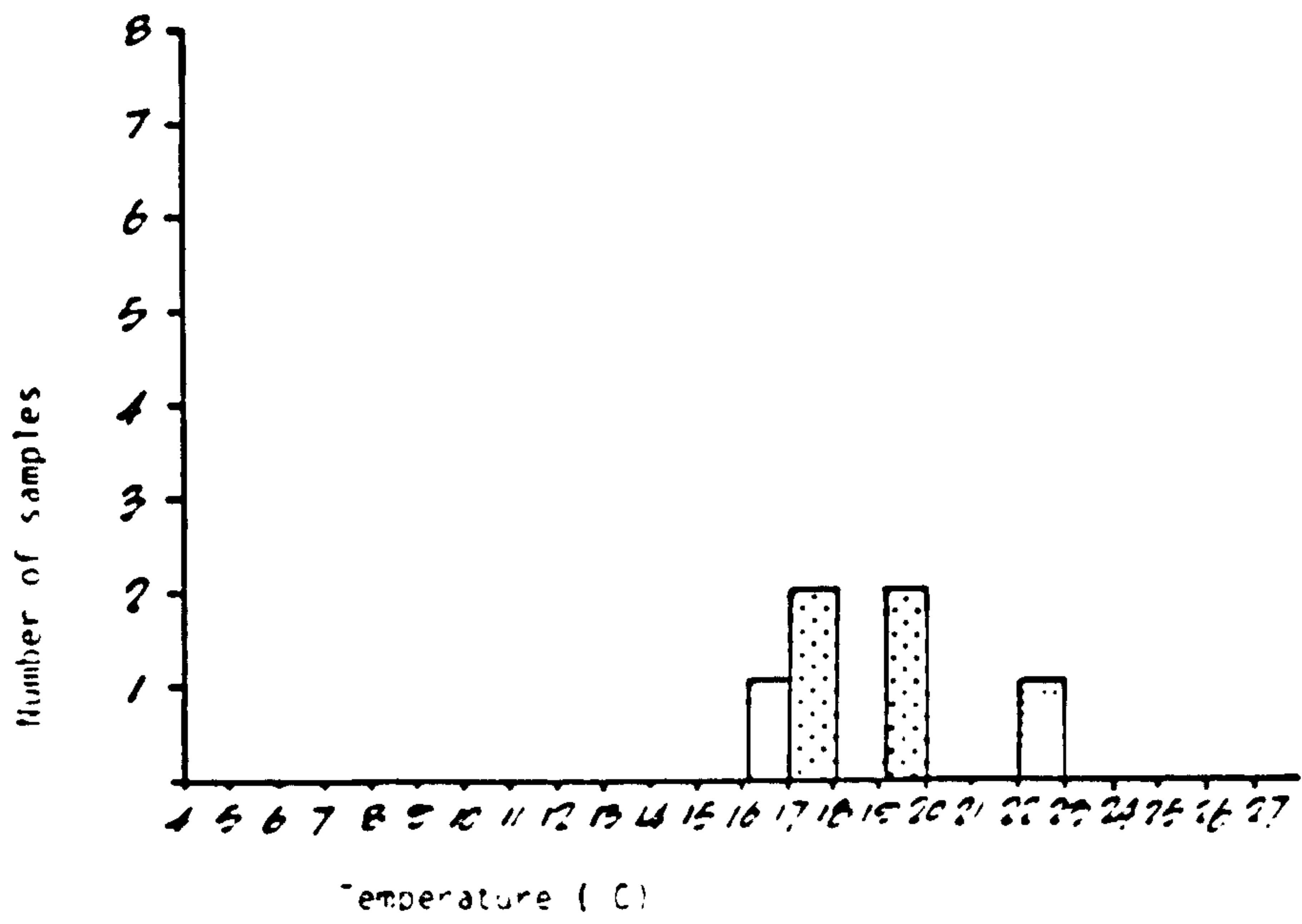


Figure 1.6b. Temperature histogram for *phaeinum* Subzone Bedfordshire, from Williams (1988, p.89).

Williams questioned the validity of the pendent life habit for *Meleagrinnella*, which Duff had proposed (1975; 1978). She also noted that *Meleagrinnella* showed a deep byssal notch, which indicated benthic attachment (see Section 4.2.4). It is clear from Williams' (1988) results on palaeotemperatures that a nektonic mode of life for *M. braamburiensis* can be discounted. It should be noted that the ammonite-derived palaeotemperatures are generally much higher than those of the benthic bivalves. However, Williams (1988, pp.95-96) thought it was a little strange that the belemnite temperatures are considerably lower than the ammonite temperatures. She does not offer any explanations for these lower temperatures; however, Martill *et al.* (1994) thought that they could have had different feeding strategies and therefore lived within a different niche. Perhaps belemnites were largely benthic or at least calcified in cooler waters (Martill pers. comm. 1997). Williams (1988) argued that the differences in palaeotemperatures between these and the ammonite *Kosmoceras* suggest seasonal thermal stratification of the water column.

Re-interpretations by Anderson *et al.* (1994) of work on the palaeoenvironments within the Oxford Clay (Williams 1988), were made using the carbon and oxygen isotopic compositions of calcareous fossils. These included: nekton (aragonitic *Kosmoceras* and calcitic belemnites) and benthos (aragonitic nuculacean bivalves and calcitic *Gryphaea*). The shell isotopic composition varied considerably within horizons but the authors could not show any obvious trends with time, which suggested that the temperature and isotopic composition of ambient seawater may have varied considerably over short time intervals but did not change systematically during deposition of the unit. Anderson *et al.* (1994, p.136) suggested that short term fluctuations were superimposed on longer-term 'stability' in this shallow-shelf environment. There was also overlap in carbon isotopic compositions between calcareous nekton and benthos, suggesting a well-mixed water column, although palaeotemperatures derived from oxygen isotopes suggested thermal stratification: *Kosmoceras* 16-20 °C, belemnites 12-19 °C with bivalves at the lower end of the belemnite temperatures. This suggested that the belemnites lived at different water depths than the ammonites which lived in the shallow waters. The belemnites were perhaps nektobenthic and the bivalves lived on the sea floor. Temperatures from the vertebrate fauna were also determined, and they showed the same range for all reptiles and fish; 20-29 °C, thus suggesting

that the majority of vertebrates lived in warm, shallow waters. Anderson *et al.* (1994, p.136) concluded that the Peterborough Member was deposited in 'normal' continental-shelf seawaters.

The overall evidence to date shows that the Peterborough Member was 'deposited in shallow water close to a humid, warm, fertile landmass that had only recently been transgressed by the sea. The main nutrient supply was terrestrial, although organic matter production was marine' (Hudson & Martill 1991, p.369).

1.2.9 Palaeogeography

The Oxford Clay outcrops at the junction of the Boreal and Tethyan ammonite faunal provinces (Callomon 1968), although little is known about the shoreline of the Oxford Sea, mainly due to concealment and/or later erosion of the formation. Hudson & Martill (1994, p.122) pointed out that there was little evidence of passage of the Oxford Clay into a marginal facies despite the abundance of driftwood and the rare presence of partially-articulated dinosaur bones within it. Only to the north nearer Humberside and Yorkshire do dominantly sandy facies appear, although these are still marine; and in the Dutch section of the North Sea, where the Oxford Clay passes into a more sandy formation with coal. An indication that land was not far from Peterborough comes from a clastic dyke intruded into the lower part of the Peterborough Member (*Jason Zone*) at Dogsthorpe. The sand in the dyke was cemented prior to compaction, by calcite precipitated from meteoric-derived water; the immediate source was the Kellaways Sand beneath the Peterborough Member.

To the south and east of the Oxford Clay sea was the London-Brabant massif - a persistent, fault bounded structural high (Hudson & Martill 1991, p.122). Although, there is no positive evidence for its emergence during the Middle Callovian, borehole evidence from Sussex and Kent (e.g. Owen 1971) has proved Oxford Clay, indicating no significant facies change towards the high. Middle Callovian clays are also present in the Bristol Channel (Warrington & Owens 1977). In the North Sea, Callovian clays have been reported in the Anglo-Dutch basin, but in the Central Graben the Callovian is represented by sands (Brown 1990).

Aspects of facies discussed by Hudson & Martill (1991, p.365) strongly suggest that the sea was no more than a few tens of metres deep. The inferred palaeogeography makes a river-derived source for the nutrients needed to sustain the productivity of the Oxford Clay sea much more likely than ocean-margin upwelling.

The immaturity of the organic matter of the Oxford Clay in the East Midlands, and the excellent preservation of aragonite, suggest only shallow burial. Estimates made by extending the younger Mesozoic cover that occurs a few tens of kilometres to the east, and geotechnical data, both suggest a maximum burial depth of approximately 500 metres at Stewartby, Bedfordshire in the late Cretaceous. The Peterborough region may have seen even less burial (Hudson & Martill 1991, p.363).

The Peterborough Member was thought to have had an early burial stage, (Hudson & Martill 1991). Pyrite formation continued into the late diagenetic stage, as some post-dates compaction of ammonite shells and septarian cracking of concretions (Hudson 1978).

1.2.10 Geochemistry

The geochemistry of the Oxford Clay has been studied by numerous authors since the 1970's when geochemical techniques began to improve (e.g., Hudson 1978, Fisher & Hudson 1987, Williams 1988, Hudson & Anderson 1989, Green 1989).

The biogeochemistry and isotopic compositions of organic and inorganic phases in the Oxford Clay has been studied in detail by Kenig *et al.* (1994). The following were determined from over 165 samples: abundance and isotopic composition of organic carbon, abundance of carbonate carbon and total sulphur, Rock-Eval pyrolysis parameters, hydrogen index (HI), oxygen index (OI) and T_{max} (maximum temperature of shales due to compaction). Data from Kenig *et al.* (1994) is used within this study to detect environmental changes within the Peterborough Member and is therefore discussed later in Section 6.4.1.

Depositional conditions of the Oxford Clay Formation through petrographic analyses of organo-mineral relationships was discussed by Belin & Kenig (1994). Belin & Kenig (1994, pp.158-159) discussed the variations in the H/C and O/C ratios, which were related to oxygen content in the water column and at

the sediment/water interface. High-TOC, high-H/C sediments of the Peterborough Member were deposited in more dysoxic conditions than the low-TOC, low-H/C sediments of the Stewartby and Peterborough Members (Belin & Kenig 1994). Belin & Kenig (1994, pp.158-159) suggested that the environment of deposition may be invoked as the major factor controlling the chemical composition of the sedimentary organic matter.

Norry *et al.* (1994) discussed the mineralogy and geochemistry of the Peterborough Member, including major elements and a range of trace elements to demonstrate that several distinct components contributed to variations within the Peterborough Member. The components found were: (1) quartz, zircon and possibly other heavy minerals, and K-feldspars, (2) carbonates, (3) phosphatic material, (4) clays and (5) organic material.

Studies on the elemental composition of fine-grained sediments are increasingly used in interpreting depositional and diagenetic environments. Norry *et al.* (1994, p.206) wanted to continue this line of work, and suggested that it was unusual that fractionation between heavy minerals and clay minerals could be demonstrated in such a fine-grained sediment, generally lacking in sedimentary structures (Macquaker 1994), and that the Oxford Clay was obviously not homogenous.

1.3 Summary

The short review of the Oxford Clay Formation (Section 1.2) shows that extensive work has been published since the end of the last century. The stratigraphy and, more importantly, the sediments of the Peterborough Member have been described in detail by numerous authors (Callomon 1968, Duff 1974; 1975, Martill & Hudson 1991, Hudson & Martill 1994 and Macquaker 1994). Correlation of these sediments has been undertaken using the ammonites (Callomon 1968 and Page pers. comm. 1997). The numerous brick pits and new landfill sites have been described in detail, stratigraphically logged and correlated using ammonite zones (Callomon 1968, Duff 1974 and Hudson & Martill 1994). The fauna of the Oxford Clay has been described (see Martill & Hudson 1991) and the Bivalvia monographed (Duff 1978). Palaeoecology (Duff 1975) and palaeoenvironmental analysis (Williams 1988, Hudson & Martill 1991 and Anderson *et al.* 1994) as well

as the recent geochemical analyses of the Oxford Clay (Belin & Kenig 1994 and Kenig et al. 1994) has been undertaken. All this previous work has given a vast amount of information on the Oxford Clay Formation, which has enabled this current study to be undertaken with ease.

PLATE 1

- A. *Bositra buchii* (Roemer 1836), left and right valves, external views, *jason* and *coronatum* Zones respectively, Stewartby pit, Bedfordshire. (From Duff 1978, Plate 4, x3.0)
- B. *Grammatodon* (*Grammatodon*) *minimus* (Leckenby 1859), left valve, external view, *grossouvrei* Subzone, Calvert pit, Buckinghamshire. (From Duff 1978, Plate 2, x 4.8)
- C. *Oxytoma* (*Oxytoma*) *inequivalve* (Sowerby 1819), left valve, external view, *jason* Subzone, Calvert pit, Buckinghamshire.
- D. *Palaeonucula triangularis* Duff 1978, left valve, external view, *obductum* Subzone, Calvert pit, Buckinghamshire.
- E. *Palaeonucula triangularis* Duff 1978, right valve, external view, *jason* Subzone, Calvert pit, Buckinghamshire.

Scale: A, x3.0; B, x 4.8.; C-E, white squares = 5 mm.

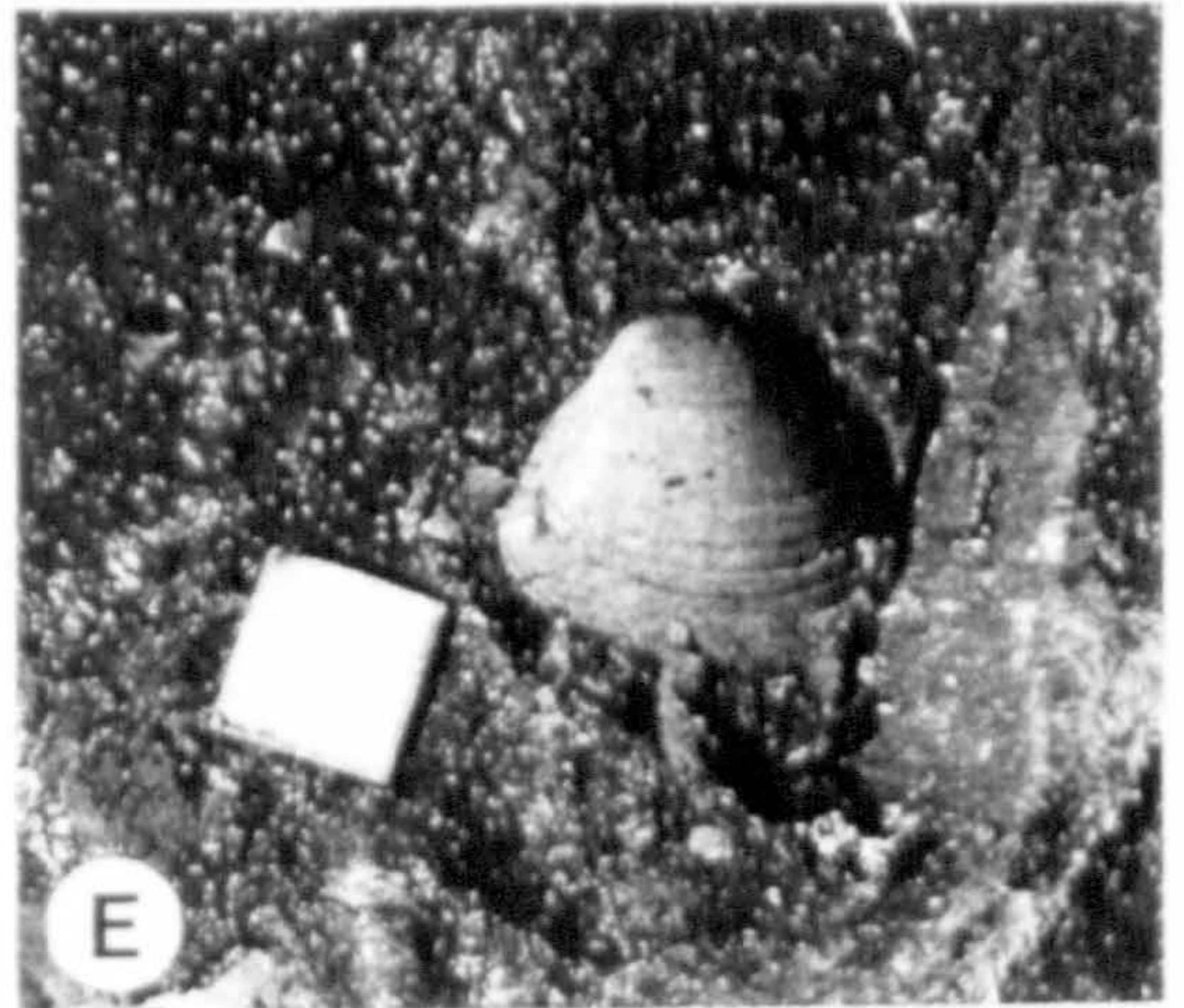
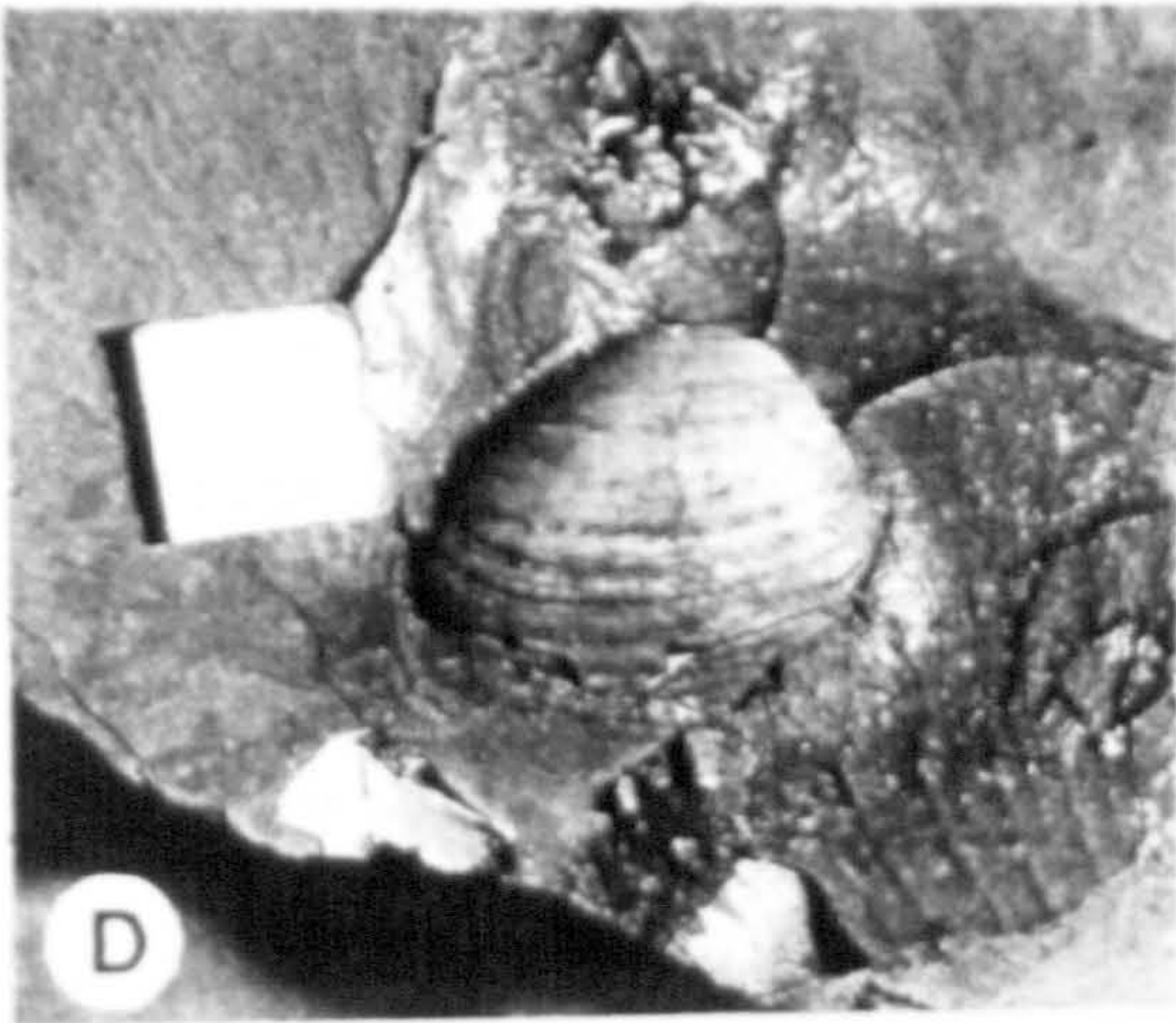
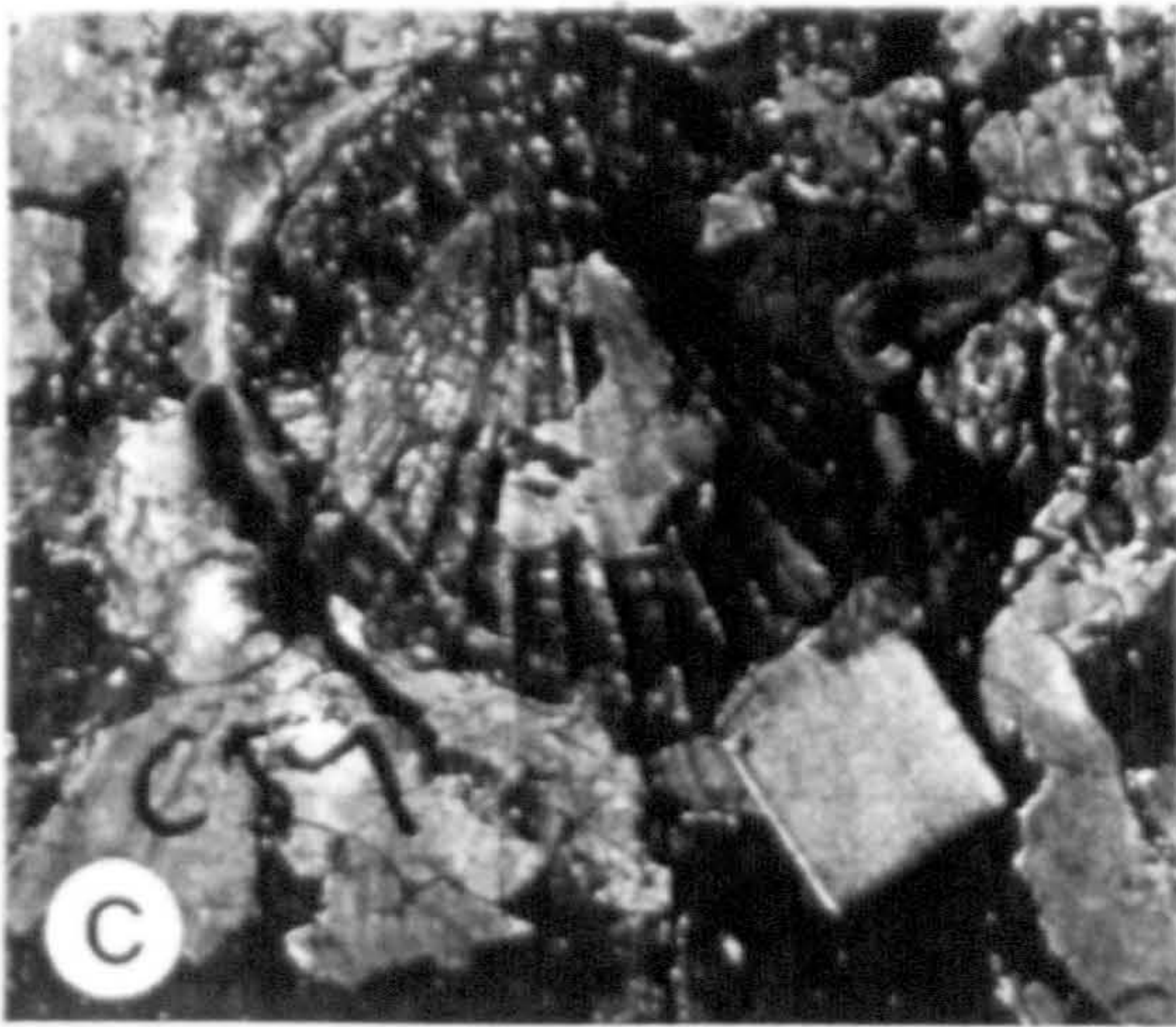
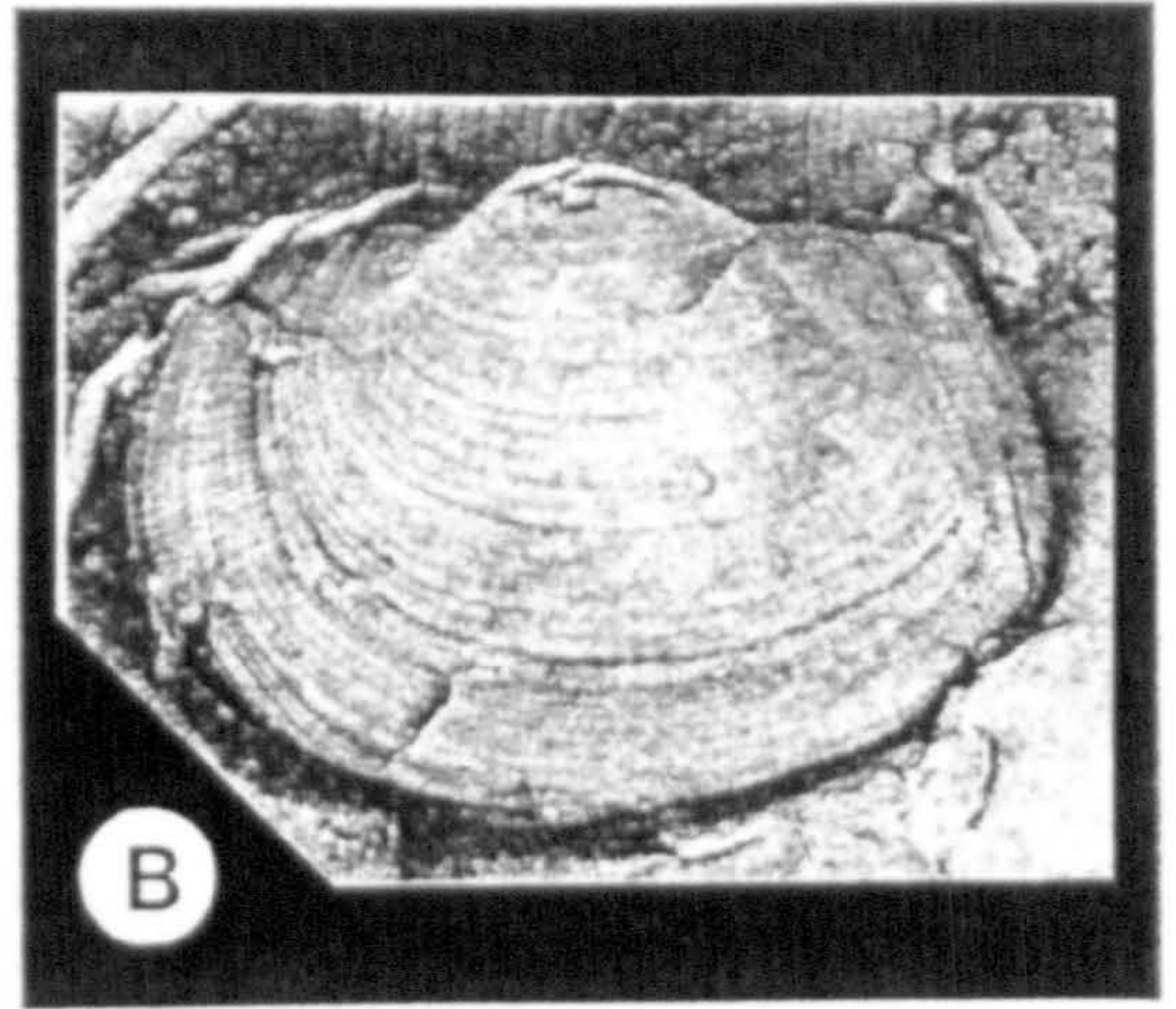
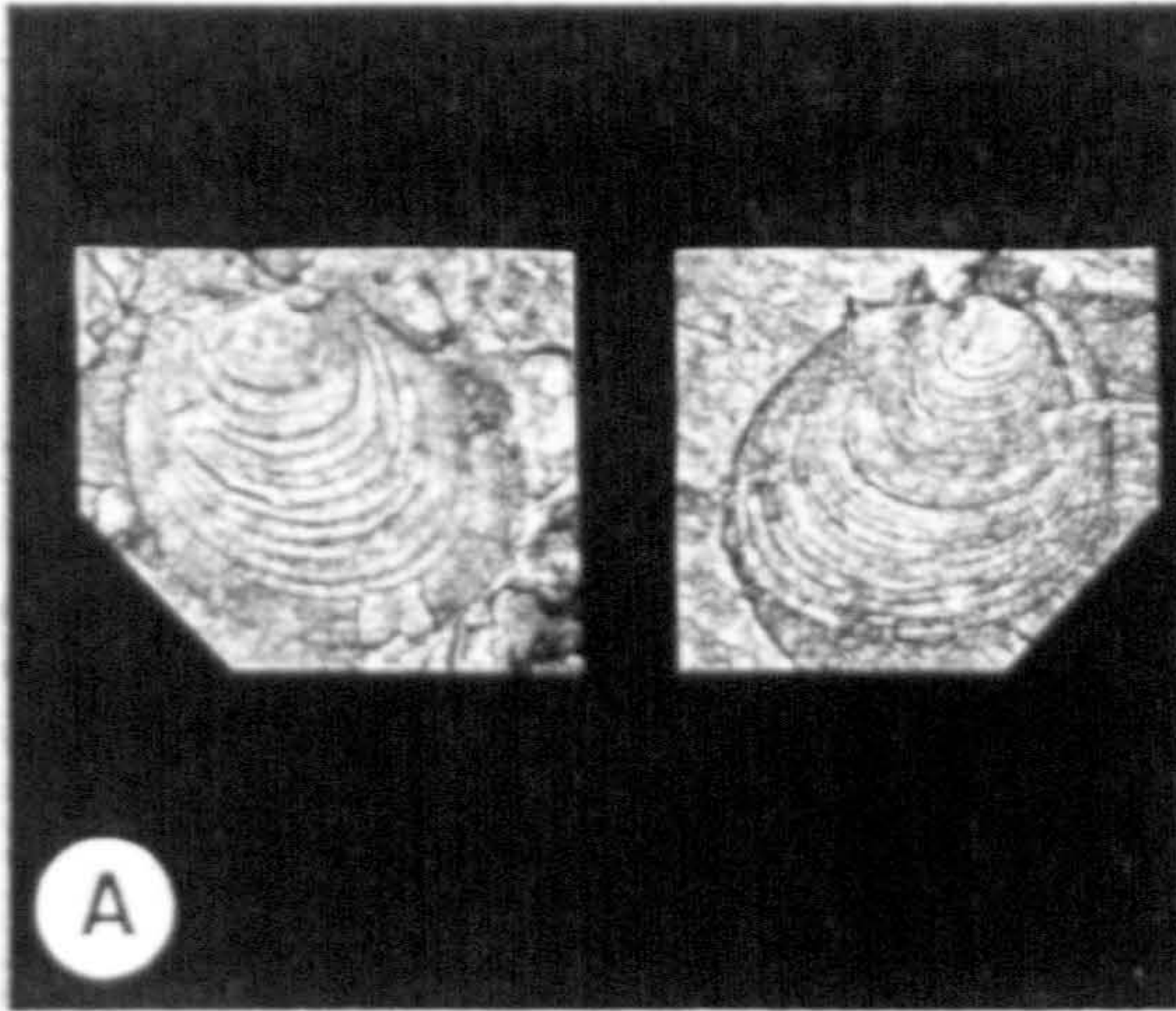
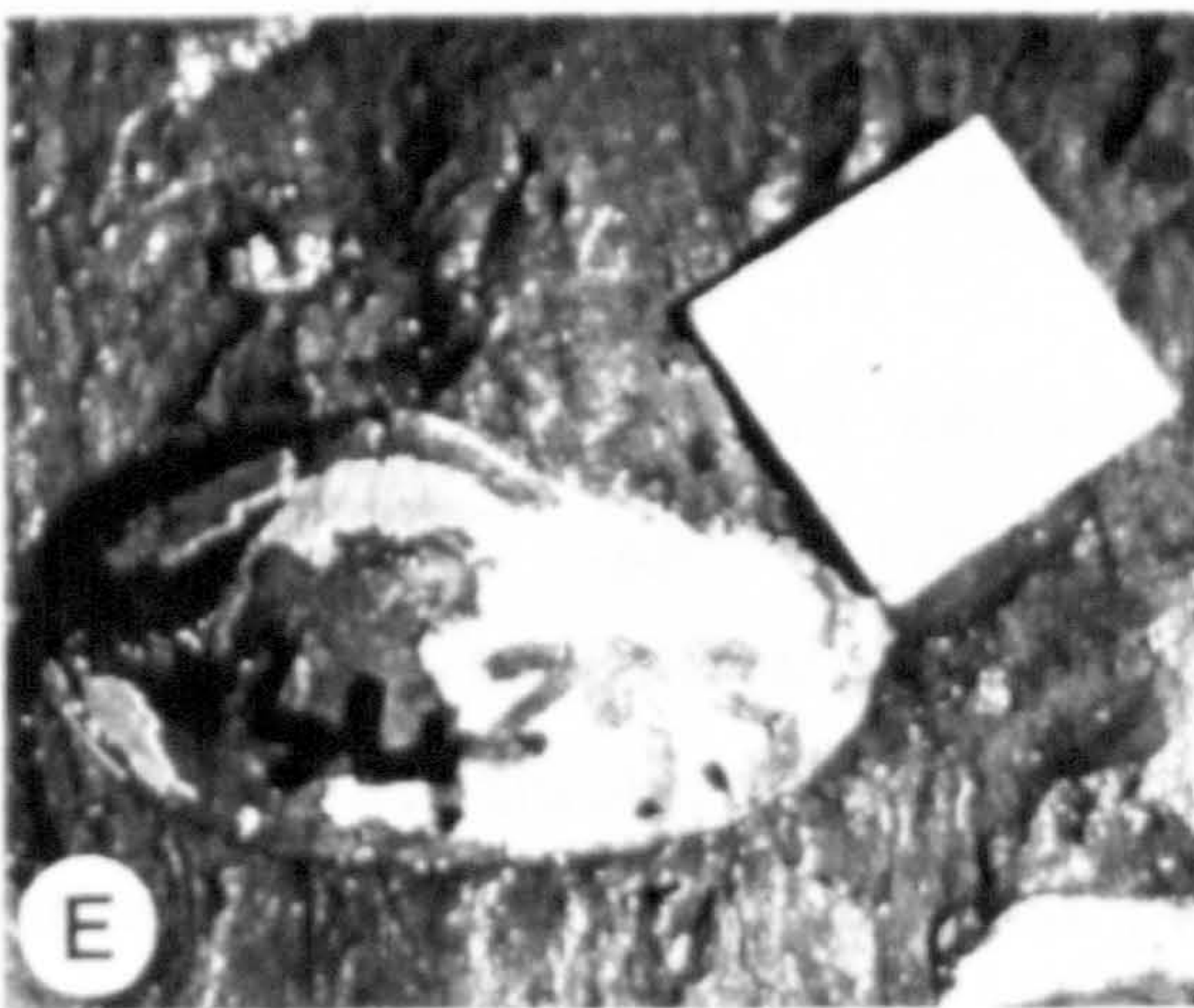
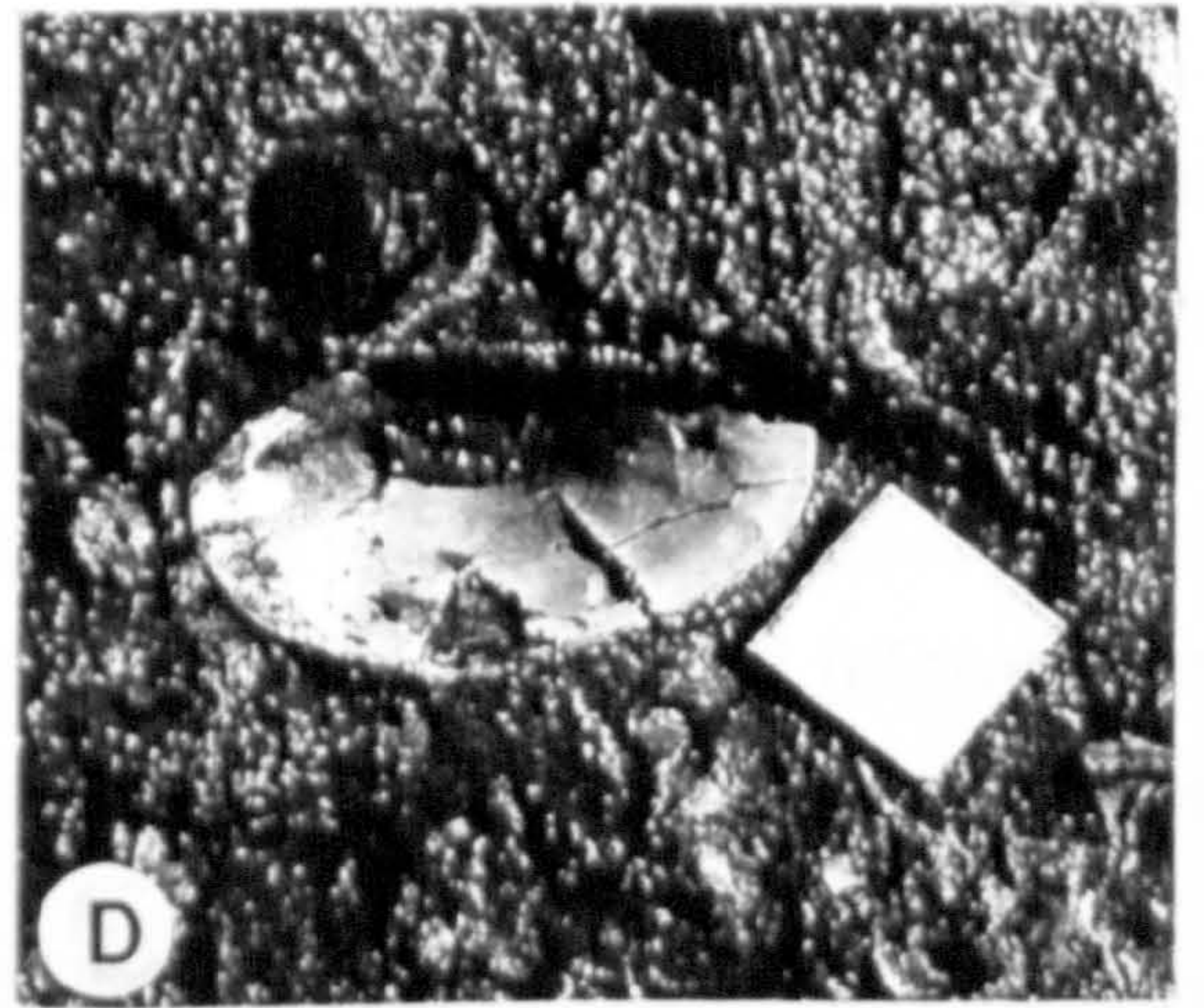
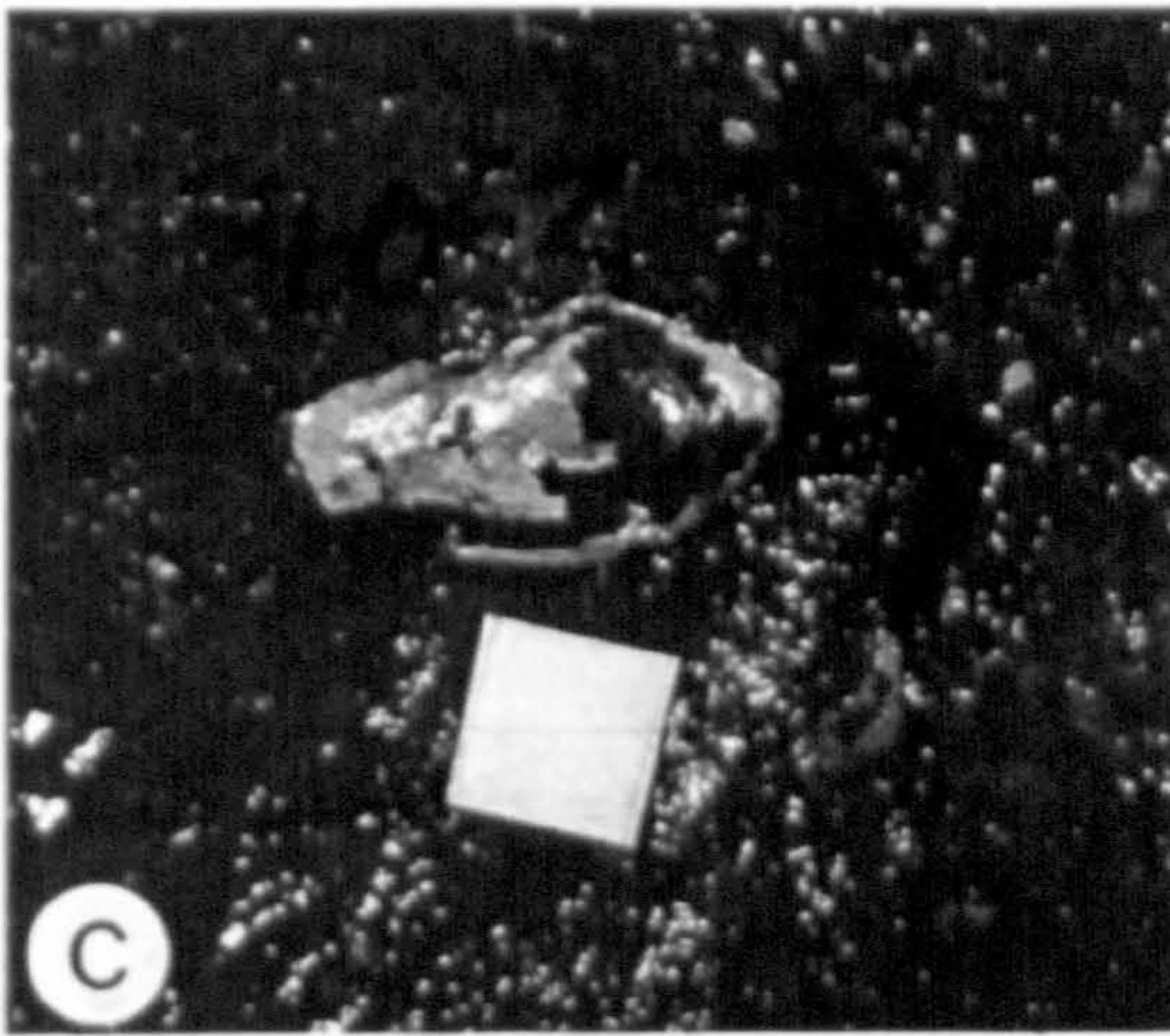
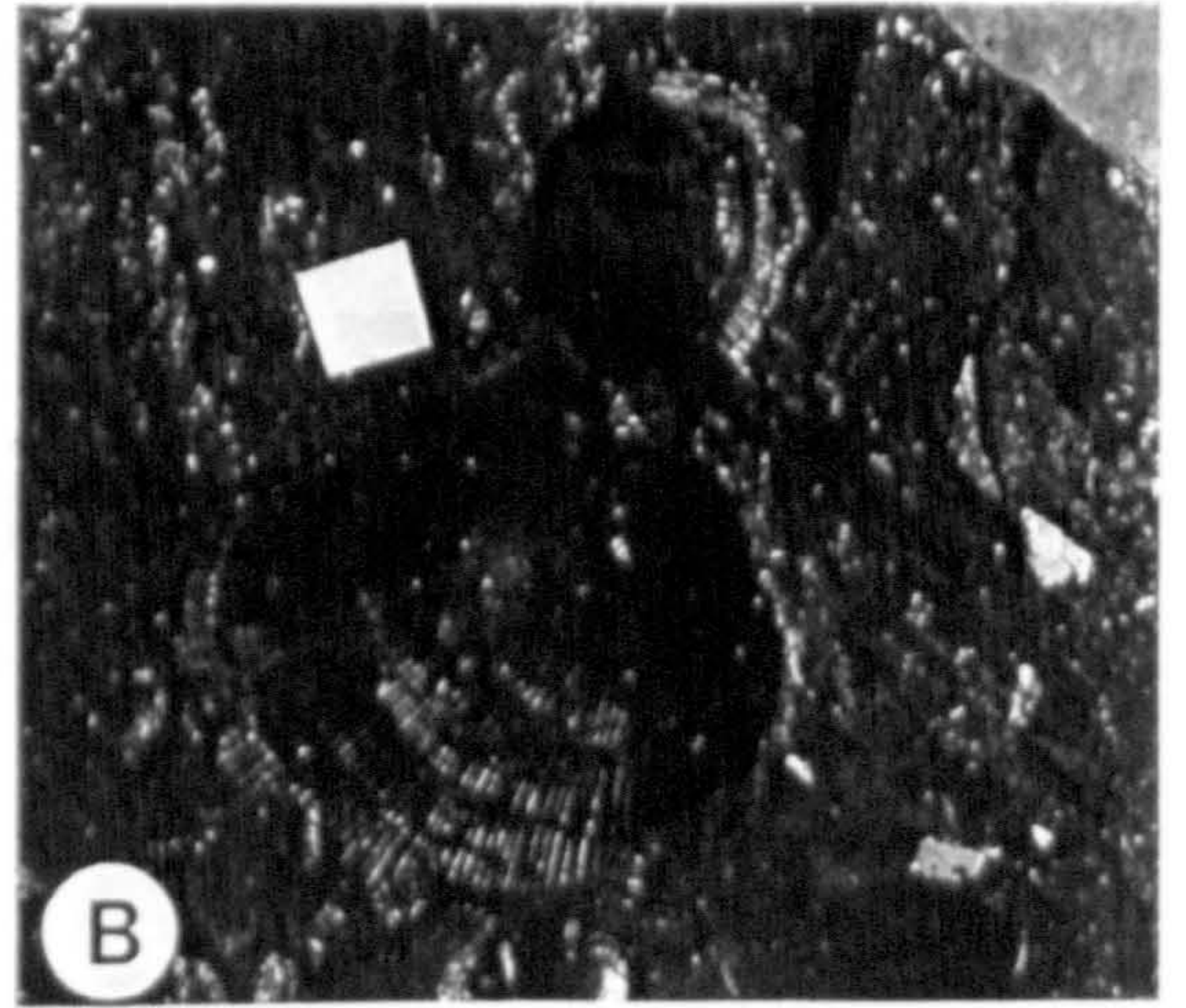
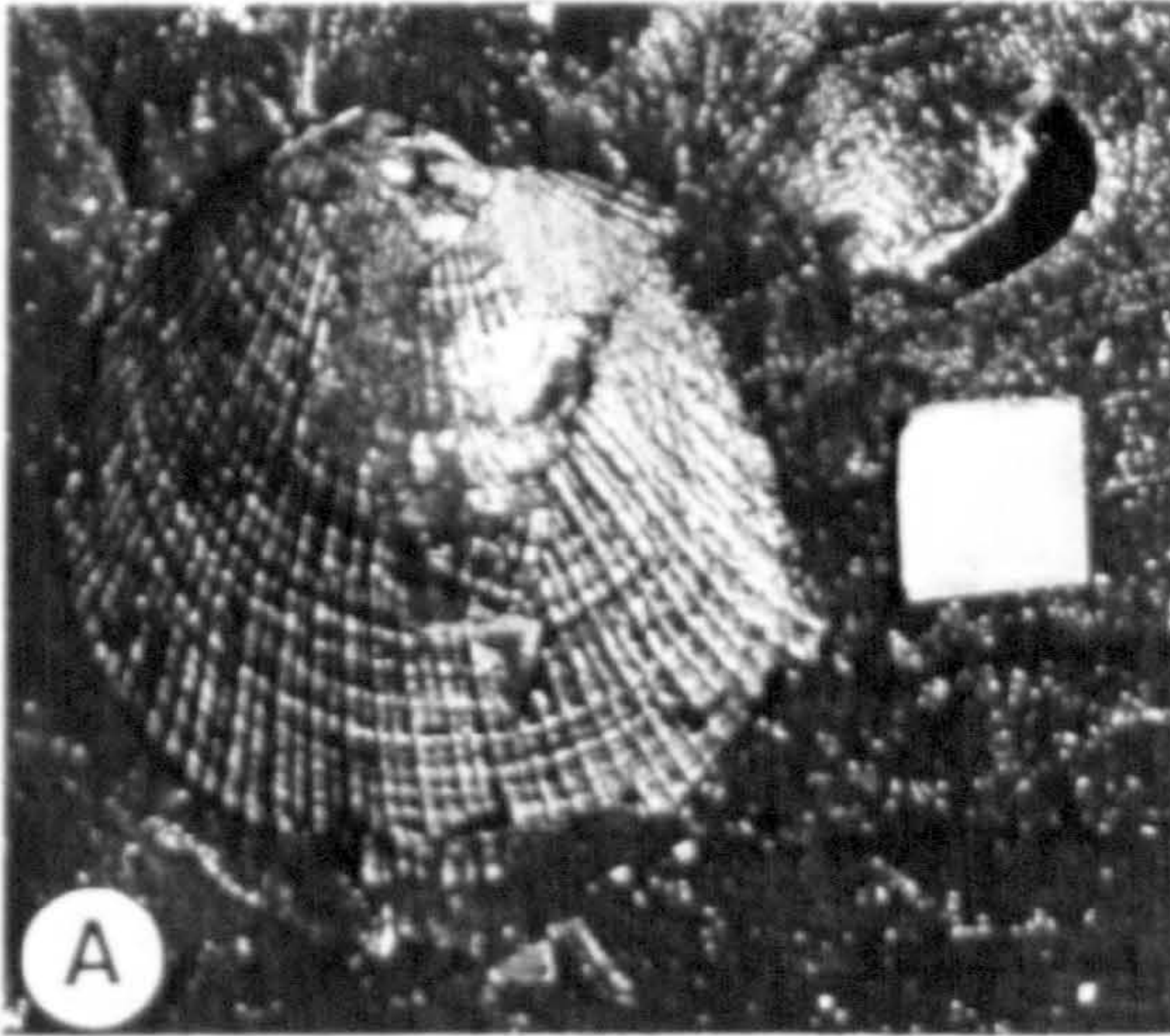


PLATE 2

- A. *Meleagrinella braamburiensis* (Phillips 1829), left valve, external view, *obductum* Subzone, Calvert pit, Buckinghamshire.
- B. *Meleagrinella braamburiensis* (Phillips 1829), left valve, internal view and right valve, external view, *obductum* Subzone, Saxon pit, Peterborough.
- C. *Mesosaccella morrisi* (Deshayes 1853), right valve, external view, *grossouvrei* Subzone, Saxon pit, Peterborough.
- D. *Mesosaccella morrisi* (Deshayes 1853), right valve, internal view, *obductum* Subzone, Saxon pit, Peterborough.
- E. *Mesosaccella morrisi* (Deshayes 1853), left valve, external view, *grossouvrei* Subzone, Saxon pit, Peterborough.
- F. *Mesosaccella morrisi* (Deshayes 1853), left valve, internal view, *grossouvrei* Subzone, Calvert pit, Buckinghamshire.

Scale: white square = 5 mm in all cases.



CHAPTER TWO

EVOLUTIONARY PATTERNS AND PROCESSES

2.1 Introduction

This chapter provides evolutionary background to this study, both theoretical and in the context for this work. The dominant theoretical microevolutionary patterns are discussed, i.e. punctuated equilibrium versus phyletic gradualism, as well as the latest theories e.g. the plus ça change model. Case Studies shown in Section 2.6 are specific to this study, giving further background information to microevolutionary patterns so far detected within the fossil record and the models they have been assigned to.

2.2 Microevolutionary patterns

2.2.1 Punctuated equilibria and phyletic gradualism - the Eldredge and Gould view

In 1972 evolutionary palaeobiology took on a new impetus when Eldredge & Gould suggested that evolutionary and morphological change did not follow the traditional Darwinian pattern of gradual change - i.e. the expectation that throughout geological time life had evolved gradually and continuously - which they called phyletic gradualism (Figure 2.1a). They quoted from Darwin's *Origin of species* (1859 first edition, p.342) 'The geological record is extremely imperfect and this fact will to a large extent explain why we do not find interminable varieties, connecting together all the extinct and existing forms of life by the finest graduated steps'. Darwin believed that there were only two ways that a new species might arise (Eldredge & Gould 1972, pp.88-89): by the transformation of an entire population from one state to another (phyletic evolution); or by the splitting of a lineage

(speciation). The second process must occur otherwise there would be no increase in the numbers of taxa and life would cease as lineages became extinct.

Eldredge & Gould (1972, p.89) ascribed the following features to the theory of phyletic gradualism:

1. New species arise by the transformation of an ancestral population into its modified descendants.
2. The transformation is even and slow.
3. The transformation involves large numbers, usually the entire ancestral population.
4. The transformation occurs over all or a large part of the ancestral species' geographical range.

These statements imply several consequences according to Eldredge & Gould (1972, p.89), two of which are particularly important to palaeontologists:

1. Ideally, the fossil record for the origin of a new species should consist of a long sequence of continuous, insensibly graded intermediate forms linking ancestor to descendant.
2. Morphological breaks in a postulated phyletic sequence are due to imperfections in the geological record.

Eldredge & Gould (1972, pp.92-93) doubted the validity of phyletic gradualism, but felt that they could not disprove it; instead they devised a new evolutionary model to provide a more adequate interpretation of the fossil evidence. They based their model on the theory of allopatric (or peripatric) speciation (Mayr 1963), i.e. the concept that a new species usually arises when a small local population becomes isolated at the margin of, or beyond, the geographic range of its parent species. Such local populations are termed 'peripheral isolates', and with time, a peripheral isolate would become a new species. Eldredge & Gould (1972, p.94) suggested that over the previous 30 years, the theory of allopatric speciation had grown in popularity, but that although palaeontologists were aware of the allopatric speciation theory, they remained too influenced by the theory of phyletic gradualism.

Eldredge & Gould (1972, p.96) called their new model of evolution 'punctuated equilibrium' (Figure 2.1b), and ascribed to it the following features:

1. New species arise by the splitting of lineages.
2. New species develop rapidly.
3. A small sub-population of the ancestral form gives rise to the new species.
4. The new species originates in a very small part of the ancestral species' geographic range - in an isolated area at the periphery of the range.

Eldredge & Gould illustrated two important consequences:

1. In a local section containing the ancestral species, the fossil record for the descendant's origin should consist of a sharp morphological break between the two forms. This break marks the migration of the descendant, from the peripherally isolated area in which it developed, into its ancestral range. As the speciation event is rapid and in a small, isolated population, we will rarely discover the actual event in the fossil record.
2. Many breaks in the fossil record are real: they express the way in which evolution occurs, not the fragments of an imperfect record. The sharp break in a local column accurately records what happened in that area through time. Palaeontologists have traditionally accepted that there is an imperfect record; however they now believe that the record is actually much better than tradition dictates.

Eldredge & Gould (1972) argued that the fossil record showed evolution occurring in sudden bursts of change (more or less instantaneous in geological time), followed by a long period of stasis. Gould (1982) suggested that 'instantaneous' was only 1% or less of the species' later existence in stasis (Figure 2.1b).

They backed the theory by their own examples (Eldredge & Gould 1972, pp.99-108) e.g. the trilobite *Phacops rana*, from the Middle Devonian (Eldredge 1971; 1972).

Numerous microevolutionary patterns have emerged from the fossil record since 1972, with the majority supporting the punctuated equilibria model. Jackson (1994) suggested cases of punctuated equilibria outnumbered cases of gradualism by 10:1. However, there are numerous biases against detecting phyletic gradualism which are discussed in Section 2.4.

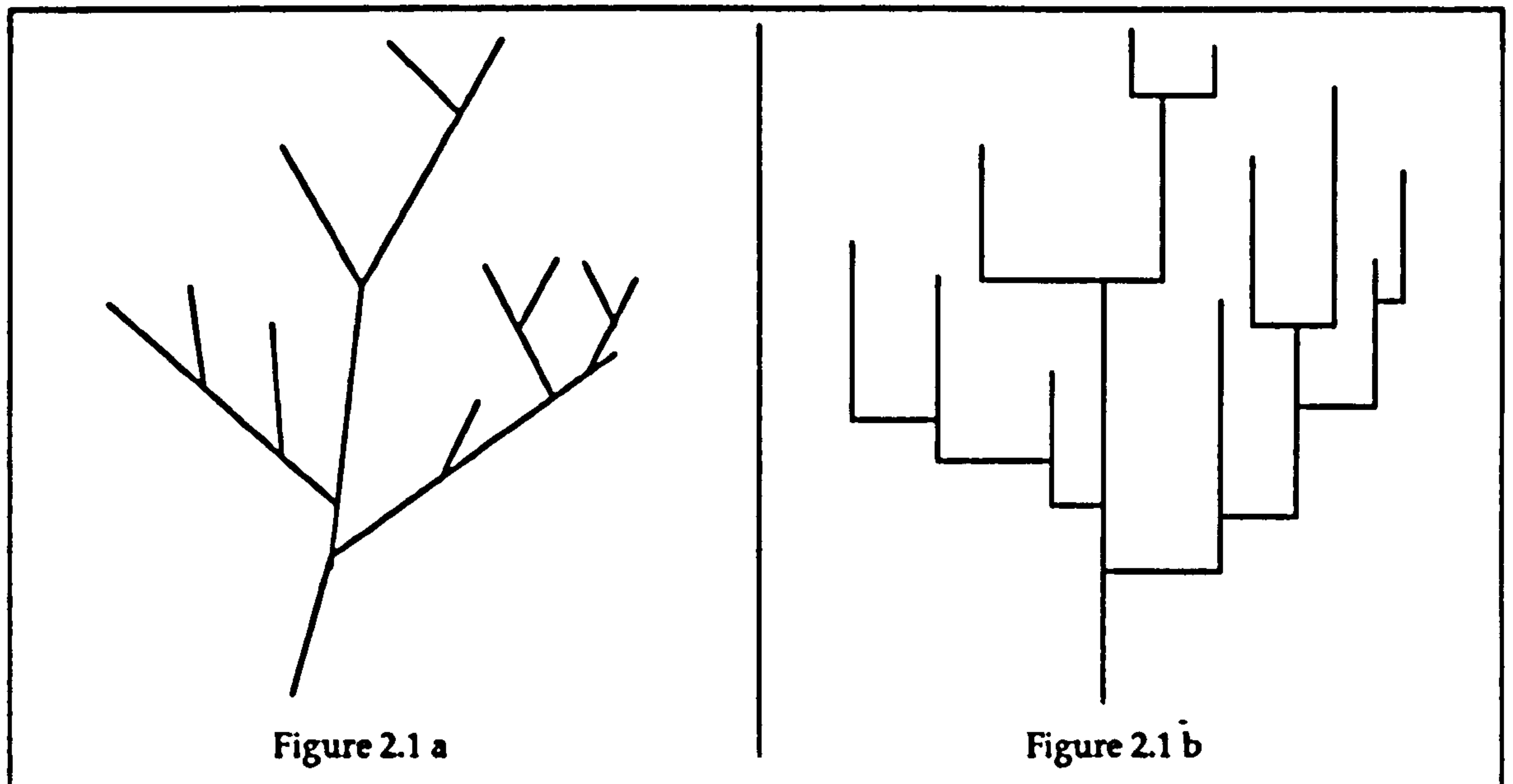


Figure 2.1a & b. Phyletic gradualism (from Ridley 1996, p.561) and punctuated equilibrium models of evolution.

Gould & Eldredge (1977, p.116) later said that their model of punctuated equilibria was 'a hypothesis about mode. We claim that speciation is orders of magnitude more important than phyletic evolution as a mode of evolutionary change' (see Figure 2.1b). They proposed that their model had tried to clarify and emphasise certain ideas, to recognise that the search for phyletic gradualism was a bad historical habit, inconsistent with current evolutionary thinking. Gould & Eldredge adopted an extreme position in attempting to show that phyletic gradualism did not exist, suggesting that Trueman's (1922) *Gryphaea* never demonstrated gradualistic change and that he never mentioned the hundreds of Liassic species that show no temporal change (stasis); that the gradual change of *Micraster* (Rowe, 1899) was not true and that Rowe did not speak about its legion of static colleagues in the English Chalk. However, both examples were written before the theory of punctuated equilibrium existed. Trueman's data were actually shown to be incorrect in the 1960's when improved stratigraphic resolution and the discovery of intermediate sections made it less plausible to ascribe patterns implying incompleteness of the fossil record (Erwin & Anstey 1995, p.13). Thus the dominance of gradualism was already declining before Eldredge & Gould's (1972) theory of punctuated equilibrium. Eldredge & Gould (1972) suggested that Mayr was one of the first biologists to suggest that evolution could be in a

punctuated style, with 'gradualism punctuated by stratigraphic gaps in which the sudden appearance of a new species in the record was to be expected *even if the record is highly complete*' (Erwin & Anstey 1995, p.14, and Skelton 1993, pp.390-391). An American palaeontologist, Simpson, also studied the fossil record but concentrated on the rates of evolution (see Section 2.3 for a further discussion on rates of evolution). Simpson questioned Darwin's surmise that rates of evolution might have been highly variable. Simpson was able to gain realistic estimates of rates of evolution, from both direct observation and from theoretical models. These observations showed that rates of morphological change, even at low levels of selection, could be expected to achieve relatively rapid transformations when perceived on a geological time-scale. Simpson therefore interpreted geologically abrupt changes in morphology in fossil lineages as representing bouts of pronounced directional selection. Simpson suggested therefore, that long periods of little or no change, could be interpreted as very weak or no directional selection (see Skelton 1993, Figure 10.20b, p.487 and pp.488-489 for further discussion on Simpson's work). Even Darwin in a late edition of the *Origin* (Gould & Eldredge 1977, p.118) said 'it is far more probable that each form remains for long periods unaltered and then again undergoes modification'.

However, Eldredge & Gould went beyond Mayr's concept of allopatric speciation (Erwin & Anstey 1995, p.14) and Simpson's work (Skelton 1993, pp.487-489), implying that microevolution in the fossil record underwent sudden abrupt change followed by these long periods of stasis, without any gradual change (see Skelton 1993, Figure 10.20c, p.487). According to Gould & Eldredge (1977, p.118), some critics (Harper, 1975; Lesperance & Bertrand, 1976) felt they were attempting to exclude gradualism by establishing a new dogma for evolutionary tempos, and in effect denied the existence of phyletic gradualism in speciation. They said that they never claimed that gradualism could not occur in theory, but emphasised their unhappiness with 'gradualism' due to the fact that stasis was ignored as 'no data' and breaks in the fossil record were treated as imperfect data. They defended their argument by saying 'If we thought that no stratigraphical evidence were needed we would not have presented quite a bit of it ourselves' (Eldredge & Gould 1972, pp.98-108). The model of punctuated equilibria does not state that evolution

cannot occur gradually at any level, it is just a theory about speciation and its deployment in the fossil record.'

Gould & Eldredge (1977) admitted that there are some valid cases of phyletic gradualism, e.g. Ozawa's forams (1975), which met all the criteria necessary for an adequate test - (1) good geographical coverage; (2) long sequence of closely spaced samples; (3) unambiguous definition of taxa; and (4) adequate biometrical testing on sufficiently large samples.

2.2.1.1 Is punctuated equilibrium testable?

It has been said by some authors, e.g. Gingerich (1987), that punctuated equilibrium is a theory that is untestable in the fossil record due to its numerous requirements. Erwin & Anstey (1995, p.17) criticised part of the punctuated equilibria model, due to the fact that it assumed that the actual geography of small isolated populations gave rise to new species. They suggested (p.17) that 'preserved fossil populations represent, at best, only submicroscopic percentages of their once-living populations. Sedimentation and preservation of sedimentary beds is a highly episodic process. Populations small enough to produce the geologically rapid morphological changes called for in punctuation have, therefore, a zero probability of preservation'. Therefore the actual speciation event is unlikely to be recorded within the fossil record, and even harder to find, making it almost impossible to test. Erwin & Anstey (1995, p.19-21) list the results of 58 studied lineages published in the last 20 years (17 show gradualism, 26 show punctuation and stasis, and 15 show gradualism and stasis). Perhaps the most interesting feature is the number of cases of gradualism and stasis which Eldredge & Gould had not considered, but which appear to be a common evolutionary pattern in the fossil record.

Gould and Eldredge (1977, pp.147-49) suggested the following when testing for gradualism vs. punctuation:

1. Study the whole geographical range of the species and do not confine yourself to a local section or single core. (However, being able to examine the whole geographical range of a taxon is very unlikely and/or impractical).

2. Study all the members of the ecosystem or community. (Again this is very difficult because of preservational problems).

The above requirements make it almost impossible to test definitively for either model. Case examples that have emerged from the fossil record (Sections 2.6.3 and 2.6.4) have rarely met the above criteria.

2.2.1.2 Further developments of punctuated equilibrium theory

In 1993 when the theory of punctuated equilibrium was 21 years old, Gould & Eldredge accepted that examples of stasis alone were not direct evidence for the strict version of punctuated equilibrium. Stasis could just be a lull in anagenetic gradualism, and replacement might represent rapid transformation without branching, or migration of a distant relative rather than evolution in situ. A good test for punctuated equilibrium, according to Gould & Eldredge (1993, p.225), 'requires (in addition to the obvious need for documented rapidity in an interval known to be sufficiently short) both a phyletic hypothesis to assert sister-group relationship of the taxa involved, and survival of putative ancestors to affirm an event of true branching rather than rapid phyletic transformation.' They admitted that these requirements are stringent, and in the light of this, and an imperfect fossil record, they were delighted that so many cases have been documented, e.g. Williamson's (1981) discovery of multiple molluscan speciation events in isolated African lakes, and Cheetham's (1986) story of evolution in the bryozoan *Metrarabdotos*. However, Williamson's molluscan data have been much criticised (see Section 2.6.3 for full details).

By 1993 there was much support for Eldredge & Gould's model, although they admitted that it is only a model and that other patterns can emerge from the fossil record. For example Johnson (1982), suggested that punctuated equilibrium should dominate in the benthic environments that yield most of our fossil record, while gradualism might prevail in pelagic realms (see also Sheldon 1987, Section 2.6.4). Sheldon (1990) proposed 'the counter-intuitive, but not unreasonable idea' according to Gould & Eldredge (1993, p.226), that punctuated equilibrium may prevail in unstable environments and gradualism in stable ones.

Gould & Eldredge (1993, p.227) did not know whether they had 'witnessed a mighty gain in insight about the natural world, or just another transient blip in the history of correspondence between misperceptions of nature and prevailing social realities of war and uncertainty.' They do say that maybe punctuated equilibrium is only palaeontology's contribution to a 'Zeitgeist and Zeitgeists (transient ghosts of time) should never be trusted'. They said 'we are either destined for history's ashheap, or we had a spark of insight about nature's constitution. Only the punctuational and unpredictable future can tell'. The second half of their proposition is almost certainly correct, that Gould and Eldredge did have an insight into nature's constitution, as seen by the numerous examples of punctuated equilibrium emerging from the fossil record.

2.2.2 Plus ça change - a new model for evolutionary patterns

'It is a general tenet of biology that major changes in the physical environment will either promote evolution or drive a species to extinction. Evidence emerging from the fossil record, however, suggests that over long timescales (e.g. a million years) the relationship between environmental change and evolution is nothing like so straightforward' (Sheldon 1994, p.47). Sheldon (1990, 1993a) suggested that continuous evolution is characteristic of relatively stable environments, whereas stasis tends to prevail in unstable environments. Sheldon's hypothesis related to physical variables that can be studied over geological timescales, such as climate changes, substrate and sea level changes. Sheldon (1996b, p.213) suggested 'intuitively, one might expect a changing environment to lead to a changing morphology, and a stable environment to stable morphology'. One of the strongest lines of evidence supporting the model is the absence of extensive speciation during the Quaternary climatic upheavals; indeed, Sheldon proposes that relatively little evolution may be occurring world-wide at present (except human induced evolution). To give but one example, *Globorotalia truncatulinoides* from the mid-Pliocene underwent its most rapid and extensive evolutionary changes between 2.8 and 2.5 million years ago, before displaying a period of stasis (Lazarus *et al.* 1995). This time interval of change corresponds only to the development of the northern hemisphere glaciation, however over the last 1.5

million years, the time of widest climatic oscillations, the foram exhibited stasis (see Section 2.6.5 for more detail).

Sheldon proposed the saying '*plus ça change, plus c'est la même chose*' (the more it changes, the more it's the same thing), which may be especially apt as far as the relationship between physical stress and phyletic evolution is concerned, and that 'more widely fluctuating environments, over geological timescales maintain their own kind of stability within wide reflecting boundaries, and selection soon tends to favour lineages with 'all purpose' hard part morphologies that are relatively inert to each environmental twist and turn. Perhaps in quieter, less dynamic environments, organisms need not be so 'generalist', in a long-term sense, and finely tuned, less time-averaged adaptations will come and go more frequently' (Sheldon 1990; 1996b, p.213). Environmental change can promote evolution but the impact of an event is entirely contingent on the long-term history of the system. The model also predicts (Sheldon 1996b, p.213) 'a tendency for more continuous evolution offshore, and in the tropics generally, and for more stasis (and occasional punctuations) in shallow waters and in temperate zones.'

Sheldon (1996a; 1996b), naming his model the '*plus ça change*' model (Figure 2.2a), proposed that 'morphological stasis is the usual response to widely fluctuating physical environments on geological timescales (until thresholds are reached). The lineages that survive in a more changing environment on geological timescales are those that are relatively inert to each environmental twist and turn, in contrast to more sensitive lineages in less changing environments'. Sheldon (1996b, p.224) went on to say 'as the vast majority of the fossil record comes from dynamic shallow marine environments, it is not surprising that many fossil lineages show approximate stasis and occasional punctuations'. He suggested that it is not surprising that cases of phyletic gradualism are rare because the environments it occurs in are so rarely represented in the fossil record. Sheldon (1996b, p.217, Figure 2.2b) predicted the pattern for a single lineage at a single locality to be 'stasis when there is greater environmental fluctuation, and net directional change and/or more widely fluctuating morphologies when environments are more narrowly fluctuating'. He also proposed that in following a single lineage through a succession, there would be more morphological variation, and

greater variability of mean morphology with time in a more stable environment, than in a more fluctuating environment (Figure 2.2b). The model is bound to have exceptions (Sheldon 1996b), and few detailed cases are yet known (see Section 2.6.5 for some case studies). Some aspects of the model however, are relatively easy to test, unlike that of the punctuated equilibria and phyletic gradualism models. This new model also unites the two older models of phyletic gradualism and punctuated equilibrium together.

Sheldon's work forms an important evolutionary context for this study. This study's aim is to detect whether microevolutionary patterns are different within the fluctuating environments and stable environments of the Oxford Clay. The plus ça change model offers some predictions of which pattern one might expect within these two different environments; however this study will try to establish the evolutionary patterns before trying to fit them into any model. Further details of the plus ça change model, including a discussion of possible mechanisms, and links to other views on stasis and change are given in Sheldon (1996b).

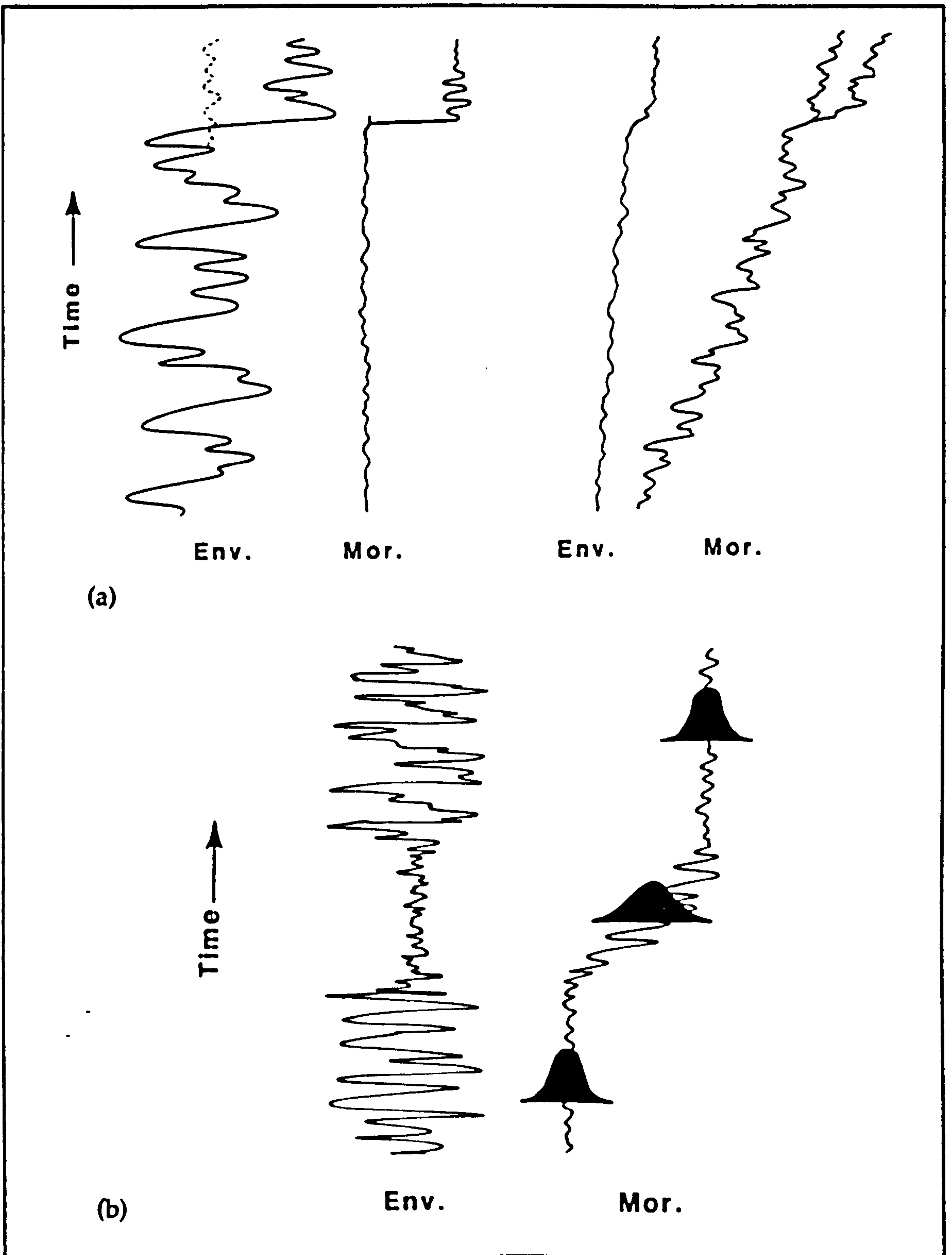


Figure 2.2a & b. In (a) the plus ça change model proposes that gradualism (right) is characteristic of narrowly fluctuating, relatively stable environments, and net stasis (with occasional punctuations) (left) is expected to prevail in more unstable environments. In (b) the predicted distribution of morphological variation is shown superimposed on the plot of average morphology. (Env. = environment and Mor. = morphology) Modified from Sheldon (1996b, pp.214 & 217).

2.3 Rates of evolution

This section considers some aspects of microevolutionary rates and illustrates some of the background to determining the rate of evolution. This is important in trying to deduce whether evolution is punctuated or gradual. Rates of evolution have sometimes been used to assess how complete is the stratigraphic record. Could fast evolutionary rates just be an indication of a condensed sequence, therefore missing out some intermediate stages? Does slow evolution indicate that the sedimentological record is more complete?

Early work on evolutionary rates by Simpson (1953) showed that moderately rapid phyletic evolution (horotely) was the norm in nature, while very fast evolution (tachytely) and very slow evolution (bradytely) were rare. Today, the dominant debate about rates of evolution focuses on the punctuational model, which holds that very slow or negligible evolution is the norm and that rapid spurts of change are rare but of great consequence. Mayr (1963) suggested that rare, localised species evolve more rapidly than abundant widespread species (see Section 2.2.1). Schopf (1981) claimed that most phyletic evolution may be concentrated in species too small and localised to be recognised or traced vertically in the fossil record.

Evolutionary rates can be measured quantitatively, as demonstrated by Gingerich (1983), and are measured in 'darwins'. A rate of one darwin over a million years would be equivalent to an average amount of change of 227%. A more fundamental discussion on evolutionary rates is given by Ridley (1996, p.553). Gingerich used this standardised unit to compare rates of evolution in quite different features from different organisms. For a discussion of the mathematical properties of the darwin see Skelton (1993, pp.501-502).

Rapid or tachytelic evolutionary rates are illustrated in a study by Gingerich (1983). From 409 estimates of evolutionary rate from the fossil record, he showed that the range of rate was between 0-39 darwins. Gingerich found that the fossil rates were significantly lower than those found in artificial selection experiments. He suggested that rates of morphological evolution documented in laboratory selection experiments, historical colonisation events, and the fossil record are inversely related to the interval of time over which there are measured. He suggested that this inverse

relationship is an artefact of comparing a narrow range of morphological variation over a wide range of time intervals, and it is also a product of time averaging. Gingerich (1983, p.161) suggested that 'rates measured over different intervals of time must be scaled against interval length before they can be compared'. This suggestion was based on a comparative study of morphological rates.

Some statistical methods were described for the detection and estimation of variability in the rate of evolution from biometrical data on single characters in fossil lineages by Charlesworth (1984a). Charlesworth proposed important questions about the pattern of evolution of a given character in a lineage; what is the amount of variation in the speed and direction of change? Do characters tend to show stasis, a steady rate of evolution in one direction, or much variability in evolutionary rate? Charlesworth (1984a, p.309) approached these questions through statistical testing of variation in evolutionary rates, and attained a quantitative measure of the amount of variation in rate. However, he found few published studies with a sufficiently large number of well characterised samples from an evolving lineage were available for the statistical methods he described. The most detailed published studies had been made on protistan microfossils (Kellogg & Hays 1975, and Malmgren *et al.* 1984). Charlesworth (1984a) suggested that it was not surprising that only one out of the six cases he analysed showed an apparently constant rate of evolution. In the other cases there was evidence for statistically significant rate variations. However, in all the cases Charlesworth analysed the periods of time were relatively short (less than 3 Ma) compared to more classical studies, e.g. Simpson (1953).

Charlesworth (1984b) developed formulae for the fraction of the population that must be eliminated by selection in each generation in order to account for a given rate of evolution in a metrical trait. He assumed a combination of directional and stabilising selection, and took into consideration the effects of competition based on phenotypic values. Charlesworth (1984b, p.320) applied his formulae to data on evolutionary rates and their variances, and was able to conclude that most selective elimination was due to stabilising selection, and that even very rapid evolutionary change in a single character usually involves low levels of additional elimination. He

suggested that long-sustained evolutionary trends are unlikely to be caused either by gradual change of the optimum under mainly stabilising selection or by the effects of competitive selection in favour of extreme individuals. It is possible, according to Charlesworth, that genetic correlations between traits under selection may limit the response of a single trait to directional selection and hence produce very gradual change.

Stanley (1985, pp.13-14) suggested that (1) 'phyletic rates are in general much slower than most evolutionists believed a decade or two ago - so slow that we must look to spurts of rapid evolution to account for the bulk of large scale transformation', and (2) 'a lot is known about how rates of large-scale evolution differ among higher animal taxa, but next to nothing is known about rates of phyletic evolution which contribute in only a minor way to large scale evolution'. According to Stanley, if rapid evolution was the norm for rare species, it was difficult to explain how in a small persistent habitat like the deep-sea vent setting, very slow net change had been the rule.

Later, Stanley (1987) argued that a valid picture of rates of evolution will only emerge from unbiased, comprehensive studies of morphology in real lineages, and that previous studies had (1) failed to assess real lineages; (2) evaluated only body size, not shape; and (3) focused only on lineages for which it was believed in advance that substantial phyletic evolution had occurred. He suggested that only two previous studies (Cheetham 1986; Stanley and Yang 1987) had assessed phyletic evolution in an unbiased and comprehensive manner, examining numerous characters for many, arbitrarily selected lineages. Stanley advised that rates of evolution should be looked at in terms of both taxonomy and morphology, and should also distinguish between rates representing shape and rates representing only size.

Ancient patterns of behaviour and coevolution were studied by Boucot (1990, p.585), who concluded that there seemed to be two modes of evolutionary rates: 'the very rapid ones associated with the rare (in geologic time) quantum-evolution events occurring almost entirely at ecologic-evolutionary unit boundaries, and the negligible ones associated with the common species-to-species level changes present within the ecological-evolutionary units into which the fossil record is divided'. Rare, endemic genera are the most rapidly evolving and have short-term durations, in

contrast to the strong correlation between widespread, abundant taxa and long-term durations. He also concluded that the smaller the population size, the greater the rate of phyletic evolution. Widespread, abundant species will most likely be preserved in the fossil record and will tend to show stasis (very slow rates of evolution).

Gingerich (1983) as already stated, observed that there was an inverse relationship between the rate of evolution and the time interval over which it is measured (see above); rapid evolution tended to be over shorter intervals of time than slower evolution. Table 2.1 below shows the rate of evolution for mammals and molluscs, over specific time intervals.

Domain	Sample Size	Evolutionary Rate (d)		Time Interval	
		Range	Geometric Mean	Range	Geometric Mean
I Selection experiments	8	12,000-200,000	58700	1.5-10 yr	3.7 yr
II Colonization	104	0-79,700	370	70-300 yr	170 yr
III Post Pleistocene Mammalia	46	0 11-32 0	3 7	1000-10,000 yr	8200 yr
IV Fossil Invertebrata and Vertebrata	363	0-26 2	0 08	8000 yr-350 Myr	3.8 Myr
Fossil Invertebrata alone	135	0-3 7	0.07	0.3-350 Myr	7.9 Myr
Fossil Vertebrata alone	228	0-26 2	0.08	8000 yr-98 Myr	1.6 Myr
I to IV combined	521	0-200,000	0.73	1.5 yr-350 Myr	0 2 Myr

d darwins yr years Myr, million years ago

Table 2.1. Gingerich’s summary of evolutionary rates, from Ridley (1996, p.556).

Gingerich (1983) corrected for the differences in time over which each evolved, and concluded that, even though invertebrates had a longer time period in which to evolve, (and appeared to evolve slowly), they actually evolved much more rapidly than the vertebrates. It is important therefore to consider the time interval when comparing evolutionary rates of lineages. If the direction of evolution fluctuates, however, the rate of evolution measured over a short interval is inevitably higher than the rate measured over a longer time interval because the short-term changes cancel out over longer times: i.e. if any fluctuations in evolutionary direction occurred (Figure 2.3), the rate measured over a shorter interval will be higher. Probably a high percentage of evolutionary lineages show some reversals. When the pattern is viewed at

low resolution over longer time periods no change at all may be apparent. Sheldon (1993, p.22) even suggested that any lineage, maintaining a range of variation, that appears not to exhibit some reversals has not been studied thoroughly enough to reveal them.

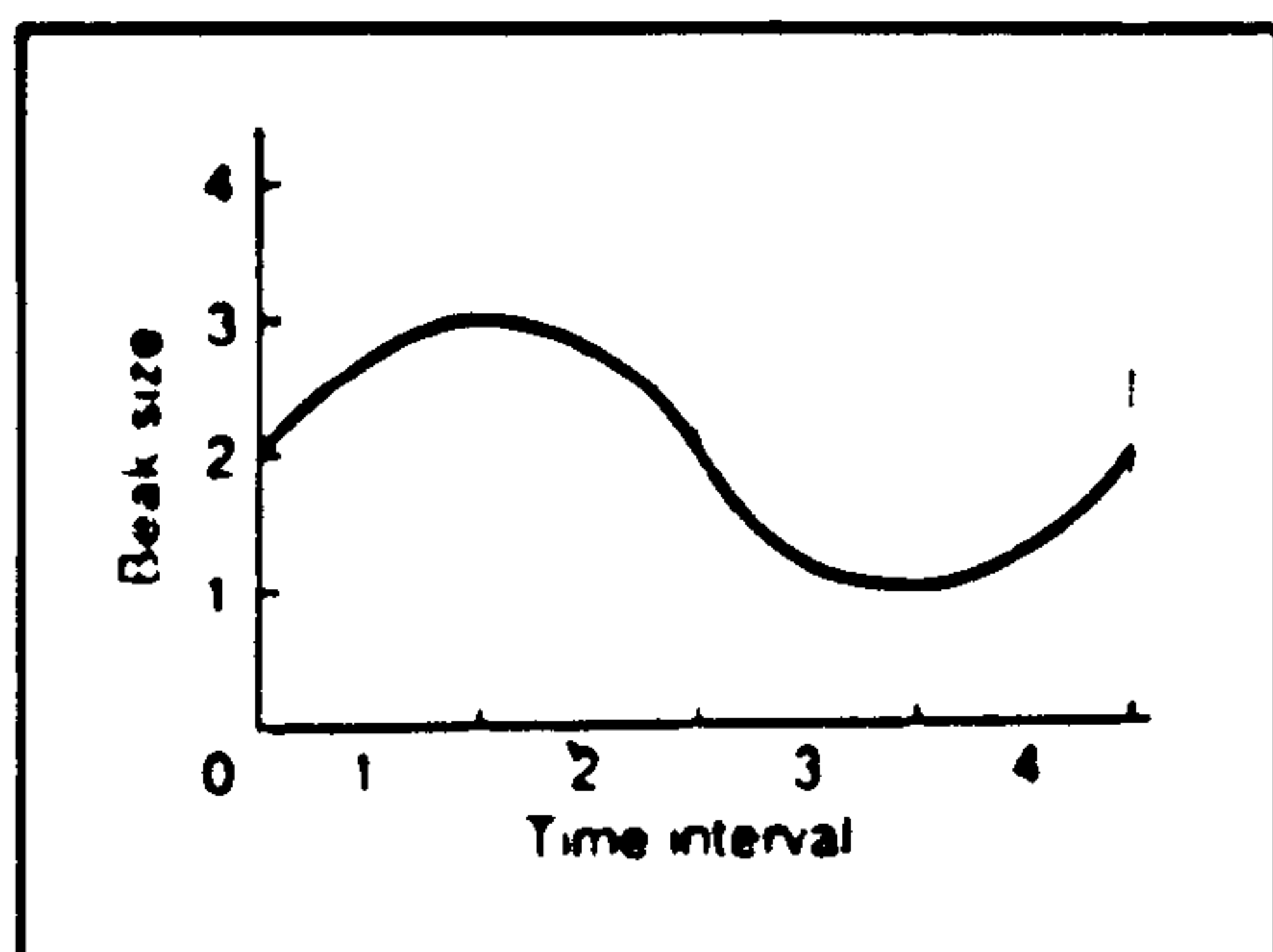


Figure 2.3. Simplified cycle of evolutionary change; the rate of change measured over short time units is higher than over the cycle as a whole, from Ridley (1996, p.559).

Do the majority of rapid evolutionary rates appear at speciation events? Ridley (1996, p.561) suggested that evolution might occur in a rapid burst, but without splitting the lineage (Figure 2.4).

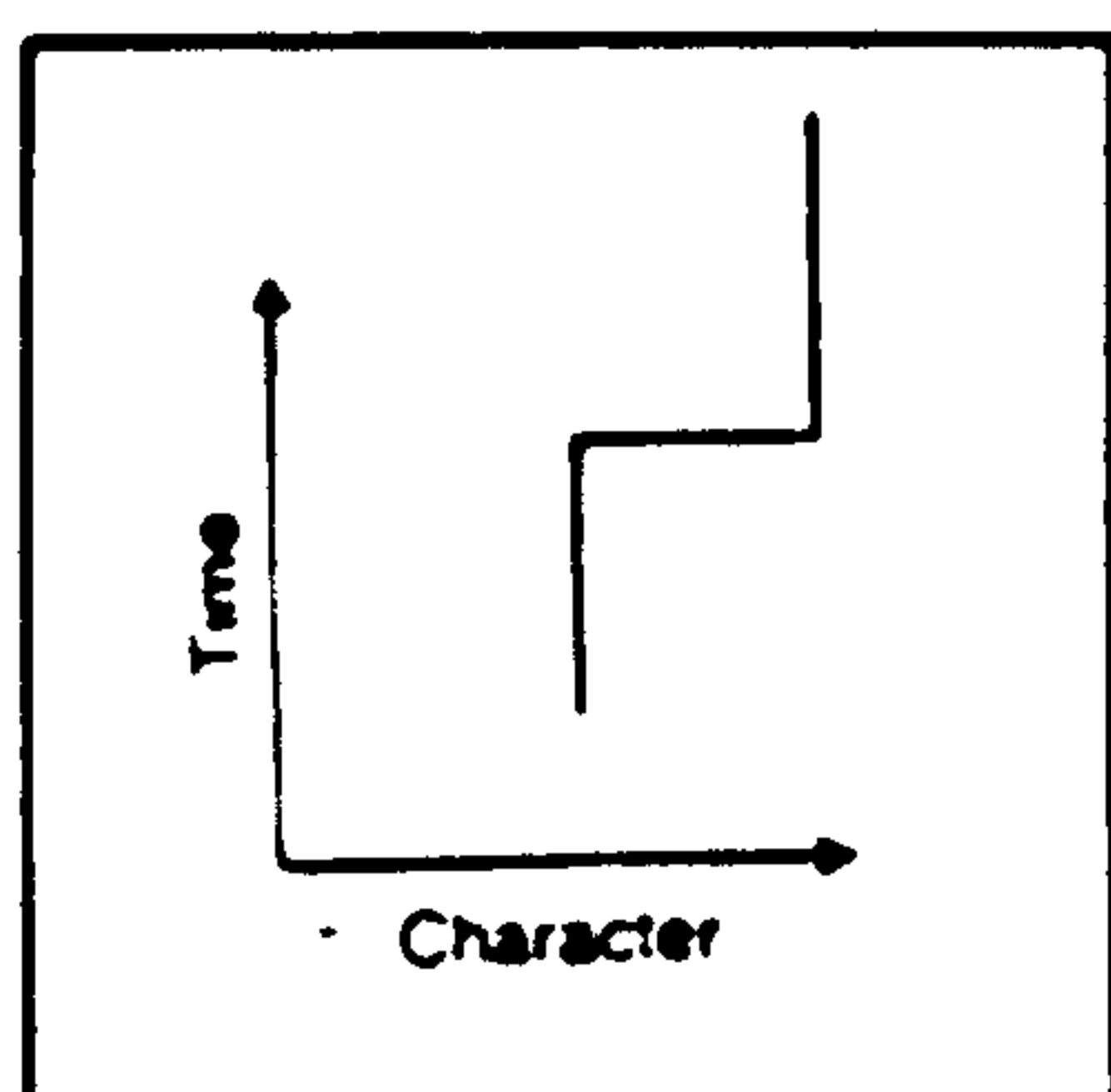


Figure 2.4. Punctuated change without split in lineage, from Ridley (1996, p.561).

This possibility was not accommodated by Eldredge & Gould (1972) in their punctuated equilibria model. In the fossil record few lineages are preserved so completely that all intermediates are seen. Whenever rapid change does occur a new species will usually be named whether the lineage has split or not (Ridley 1996, p.567). Sheldon's (1987) trilobites are a good example; fossils at the beginning and end of the lineage had been previously described as different species. Intermediates were then found and a case of phyletic gradualism emerged, with no evidence of lineage splitting. This questions the validity of

other cases illustrated from the fossil record, and whether they were in fact thoroughly investigated or not. However, decisive evidence for or against Eldredge and Gould's idea that rapid evolution is usually confined to the times of lineage splits remains to be found (See Erwin & Anstey 1995, p.28-31).

The rate of sedimentation is a very important factor in determining the type of evolution. However, as yet no study has been undertaken to observe the rate of change within continuous characters and linked this with the completeness of the sedimentological record. Macleod (1991) and Ridley (1996) suggested that perhaps higher rates of evolution would be observed within condensed sections (where intermediates are missing and a gradual trend might be mistaken for a punctuated event), and conversely slow rates of evolution would be observed in nearer complete sections (low rates of evolution giving a picture of either stasis or gradualistic change). It would be interesting to investigate the apparent rate of evolution in successions with high stratigraphical completeness. A more stable environment, with fewer sedimentary hiatuses, and therefore greater stratigraphic completeness, should, other things being equal, show slower apparent net rates of evolution. A more fluctuating environment, with more sedimentary hiatuses in a condensed sequence, might show faster rates of evolution.

2.4 Biases in the fossil record

The majority of the biases in the fossil record occur due to human factors, e.g. descriptive error or inadequate sampling. Sheldon (1993; 1996b) discussed many of these such biases:

1. The requirement to apply binominal taxonomy (i.e. Linnean names) to fossils. This often forces people to put specimens into discrete species rather than name a new intermediate species or imply uncertainty; see point three.
2. The amalgamation of specimens from different stratigraphic horizons in order to collect enough material for full descriptions and statistical treatment. This merges any evolutionary change over that time interval including any net directional change and reversals, or a change of variance - all this will be submerged within one large range of variation.

3. A reluctance for people to use terms implying uncertainty of identification, i.e. *aff.*, *cf.*, or *?*. This may be interpreted to mean that the worker has not made the effort to name the fossil correctly. However, it might actually reflect the presence of an intermediate stage.
4. An absence of formal nomenclature to signify small morphological differences between samples from different stratigraphic levels. There is no accepted method to denote intermediate morphology between subspecies.
5. Plotting species ranges on range charts as vertical lines.
6. Cladistic methods of phylogenetic analysis.

Problems of biases affecting the perception of morphological patterns are also discussed by Erwin & Anstey (1995, pp.23-24); they used the example of Ozawa's (1975) Permian protozoan fusulines. Ozawa suggested that nine measured characters showed gradualism, whereas Gould & Eldredge (1977) considered only four to show gradualism. Other biases Erwin & Anstey suggested were the statistical methods used, e.g. logarithmic transformations used by Gingerich (1976; 1985). Logarithmic data can be misconstrued by people who do not understand them. The data used in the studies by Gingerich were perfectly valid, it is only the interpretation of the logarithmic data which can be misleading, and therefore we need to be wary of interpreting logarithmic data.

Within this study the real data (actual morphological measurements) were graphed against stratigraphic height in order to look at the evolutionary pattern. No logarithms or statistical analysis such as multivariate analysis were performed when illustrating morphological change.

Perhaps one of the most common biases is gaps in the fossil record (both vertically and laterally) generating an impression of abrupt change. The more incomplete the stratigraphic record the more likely that intermediate forms will not be recorded, irrespective of the pattern of evolution. Despite all these biases obscuring the true pattern, both gradualism and approximate stasis do seem to be a common feature of the fossil record (see Sheldon 1987, Johnson & Lennon 1990, Johnson 1993, and Erwin & Anstey 1995, pp.19-21 for other examples).

2.5 Evolutionary reversals

Another major bias that has hindered the perception of evolutionary patterns is an expectation not to envisage reversals. Sheldon (1993, pp.21-22) discussed four main points which are adapted here.

1. Dollo's Law, generally phrased as 'evolution is irreversible'. This was meant to apply to the whole organism, not individual characters, the majority of which can exhibit evolutionary reversals (for example see Figure 2.5).
2. The textbook description of phyletic evolution as unidirectional change. Note how diagrams in textbooks contrasting phyletic gradualism with punctuated equilibria show no reversals at all. This has even been the case in Ridley's (1996) second edition of 'Evolution' published only last year, see Figure 2.1a, and compare this to Figure 2.6, which has been drawn with reversals.
3. Occam's Razor; the principle of parsimony. Unlike the Roman road builders, evolution does not follow a straight line course, and it, of course, has no purpose. A straight line, implying unidirectional evolution at a constant rate, is highly improbable, yet this is the most frequent theoretical representation of phyletic change (see Figure 2.6 for a more realistic representation of phyletic gradualism).
4. Orthoselection; evolutionary trends remain fairly constant over long periods of time. Note here that the important factor is the time length involved. Even a random walk over a long period of time will look more like stasis or directional trends with the reversals smoothed out.

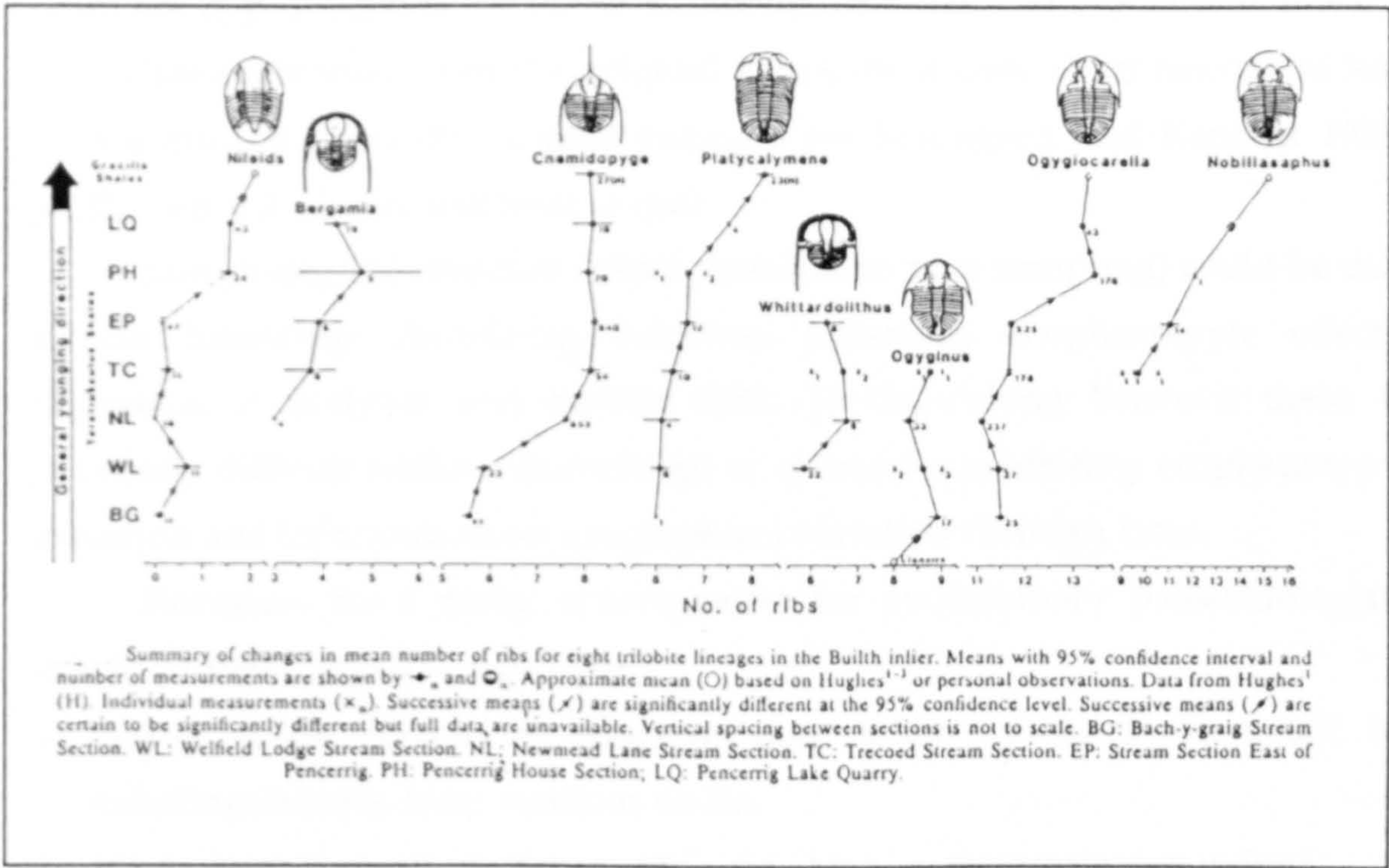


Figure 2.5. Gradualistic trilobite data, from Sheldon (1987, p.562).

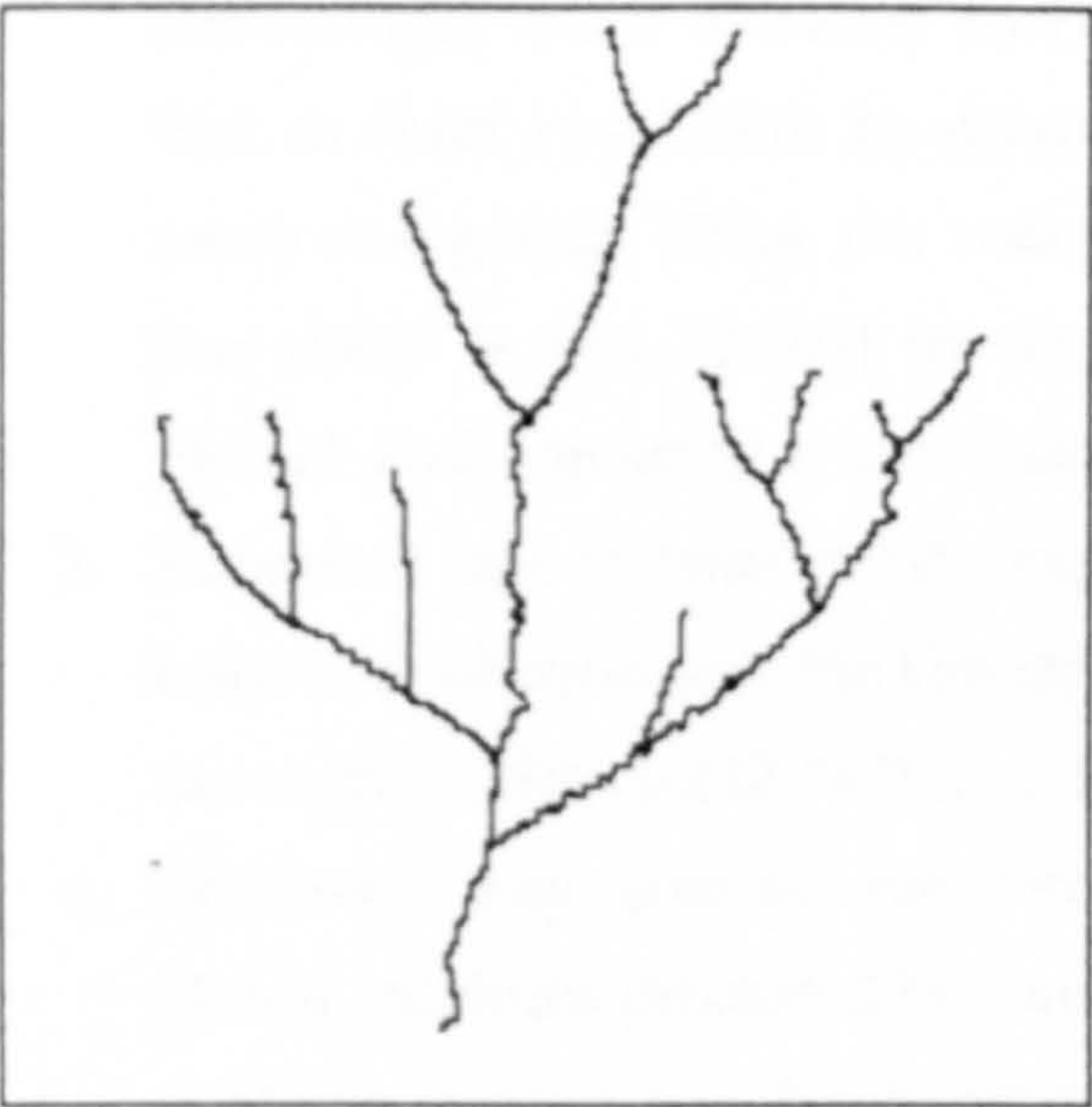


Figure 2.6. Phyletic gradualism, with reversals.

According to Sheldon (1993) 'Straight-line evolution is a very special case, like drawing one random walk and expecting evolution to follow that particular pattern'. He stated that he did not know of any cases of high resolution studies of an individual fossil lineage that represent this. I am also unaware of any such cases. Even when a lineage is said to be in stasis, this means there is no net directional change, and that the beginning point and end

point are approximately the same. However, one will still expect that lineage to deviate somewhat from the original value, even over short periods of less than a million years (For a good example see Malmgren and Kennett 1981, p.235, Figure 2 - mean apertural shape).

Morphological reversals (other than due to poor sampling) could be due to the following: fluctuating selection pressures, ecophenotypic effects, migration of ecotypes and genetic drift. Distinguishing between these is extremely difficult without knowledge of characters exhibiting ecophenotypic variation and information on geographical variation through time.

Reversals have many consequences for evolutionary palaeobiologists (Sheldon 1993, pp.24-25) including:

1. Many trends driven by selection may when resolved in detail be indistinguishable from random walks.
2. Most evolutionary patterns will be highly timescale-dependent and sensitive to data amalgamation, given reversals. Patterns will become increasingly more dynamic when timescales become finer. It is easy to see that as finer resolution is approached then the pattern emerging will be more changeable. Thus, the coarser the timescale the worse the resolution: fine detail is lost, almost ironing out all the creases, leaving a smoother pattern and obscuring any reversals.
3. Reversals can at least partly explain the relationship between measured rates of evolution and the timespan under consideration (Section 2.2.2). See Levington (1988, p.342-347) for a further discussion of this point.
4. Reversals may account for some cases of 'iterative evolution', e.g. the olenid trilobites discussed by Kaufmann in 1933. These short-lived lineages showing similar trends are assumed to have budded off repeatedly from a hypothetical unchanging stock. Sheldon (1993, pp.21-26) discussed this more fully and gives examples of ignored reversals in the fossil record.
5. Reversals do, however, make it more difficult to subdivide a lineage into successive chronospecies. The more detailed the pattern, the more difficult to subdivide the lineage; see Sheldon's (1987) Builth trilobites (Figure 2.5), and Bell's *et al.* (1985) stickleback fish *Eucryrtidium* in Skelton (1993, Figure 10.23, p.495) for good examples.

6. Jumps in trends cannot be used to indicate the amount of time missing or unrepresented in the strata, as reversals can exist (and in any case one can not assume a constant rate).
7. Reversals complicate the theoretical arguments concerning differentiation between gradualistic and punctuated patterns and have often been omitted in the past from consideration. The famous study by Bell *et al.* (1985) documents reversals in Miocene sticklebacks. However, it is Sheldon (1993; 1996b) that has really highlighted the need for reversals to be taken into consideration.

Examples of microevolutionary studies showing reversals include: Brinkmann's (1929) *Kosmoceras* data (Raup & Crick 1981), the *Globorotalia tumida* foraminifera lineage (Malmgren *et al.* 1983), foraminifera, corals and molluscs at the onset of northern hemisphere glaciation about 2 million years ago (Jackson 1994), and the Lower Jurassic *Gryphaea* (Johnson 1994).

In summary, reversals play an important role in the pattern of evolution, ignored reversals are ignored data, very much the same way as stasis was once ignored as 'no data'. Reversals do complicate the argument between phyletic gradualism and punctuated equilibria, but perhaps this will make palaeontologists look at the real patterns emerging and not try to fit the pattern into a specific model.

2.6 Relevant case studies concerning microevolutionary patterns

2.6.1 The Brinkmann study

Brinkmann in 1929 studied in great detail the *Kosmoceras* ammonite fauna of the Peterborough Member, Peterborough. The main aim of his work was to record accurately the chronological distributions of fossil organisms, species characteristics and vertical life-span. The *Kosmoceras* genus was split into the following subgenera by Brinkmann (1929): *Zugokosmoceras*, *Anakosmoceras*, *Spinikosmoceras* and *Kosmoceras s. str.* They were split further into species which are now used to index some of the ammonite zone/subzones (see Section 3.5.1).

Brinkmann (1929) investigated the following features: final diameter of the shell, final peristome (dimension), final whorl height, final umbilical diameter, final whorl width, apertural proportion (whorl height divided by the whorl width), and the number of ribs on tubercles. He quoted the accuracy of his morphological measurements as not exceeding a standard error of 1.5-2%. Only the diameter at which the ribs fade out is probably less accurate at around 3% error.

Brinkmann worked from 3 pits near Peterborough. The first was a London Brick Company pit, south of Fletton. The oldest beds were investigated in this clay pit, and fossils of levels 0-135 cm came from here (Brinkmann split each of the pits into levels of 1 cm, with 0 cm at the base of each pit). The second clay pit is that of the old Itter Brick works in Kingsdyke (now owned by Hanson Brick PLC). Fossils from the level 100-565 cm were sampled from here. The third clay pit was owned by London Brick Company, and was situated between Kingsdyke and Whittlesey. Brinkmann sampled mainly from the younger beds, with a fewer older ones, although in total levels 300-1310 cm were involved.

Brinkmann began work by establishing a base point three-quarters of a metre below the floor of the clay pit near Fletton. Brinkmann then established further fixed points up the face, usually provided by the shell beds. The entire stratigraphic sequence (13 m) was divided into over 1300 stratigraphic levels, with ammonites collected and recorded to the nearest centimetre (see Section

7.11 for description of section). Brinkmann (1929, p.26) thought that the precision of determining stratigraphic level was about 3-5%. Once the stratigraphic level was determined the taxonomic classification was defined and then measurements were taken to the nearest millimetre. (Over 3000 ammonites were measured).

Although Brinkmann (1929, p.26) recorded the stratigraphic level of the ammonites accurately, there are some problems with his methods. Brinkmann collected from different stratigraphical levels from the three different pits (as described above), with overlapping collections. However, there is a distance of 8 km between Fletton and Kingsdyke. Brinkmann suggested that the sediment thickness, fossil contents and sedimentary composition had no changes over the 8 km. Macquaker & Howell (in press) have shown that over a distance of just 1 km (between Saxon and Kingsdyke pits) there are changes in the sediment and sediment thickness. Therefore, over a distance of 8 km there would almost certainly be considerable changes in the sediment thickness and fossil contents. Therefore the stratigraphical level, of each ammonite to the nearest 1 cm, may have been very inaccurate when comparing across these three pits. Within this study the section dug in Saxon pit was a continuous section from one locality.

The main conclusions of Brinkmann's work were that the evolution of the four lineages was broadly parallel (see Figure 7.91). Brinkmann (1929, p.218) said 'the kosmocerotid lineages form a natural unit, living in the same conditions and evolving through time in a parallel fashion, whether due to a similar genetic substrate inherited from their ancestors which then unfolded in the course of time, or to a similar reaction to the same environment.' Brinkmann's work is important to this study as he is the only other person to have carried out a microevolutionary study on the Oxford Clay Formation. This therefore gives the opportunity to compare the results from this study with his (Section 7.11). Brinkmann showed that there are jumps within the morphology of the kosmocerotids, which were either due to missing intermediates or an evolutionary jump. These jumps in the morphology will be compared to the morphology of the bivalves from the same stratigraphical position within the Peterborough Member.

2.6.2 Raup and Crick's re-evaluation of Brinkmann's work

Raup and Crick (1981) re-evaluated Brinkmann's (1929) work in order to analyse one aspect of *Kosmoceras* evolution: the evolution of single characters through time. Raup & Crick asked: (1) how significant are the changes in terms of the formation of new species? and (2) what evolutionary mechanisms brought about the changes?

The second question of Raup & Crick is particularly relevant for this study as the mechanisms believed to be responsible for evolutionary changes within the kosmoceratid lineages could have affected the bivalves too.

Raup & Crick (1981, p.205) interpreted the kosmocerid evolution in at least three alternative ways: (1) rapid change as part of a punctuation event; (2) longer term phyletic change leading to the formation of new species (phyletic gradualism); and (3) rather aimless fluctuation in morphology characteristic of a steady state condition (stasis) in a species in the interval between punctuation events. Raup and Crick (1981) concluded that there was too much time involved to consider the entire section as recording a single punctuation event, ruling out the first interpretation. They considered phyletic gradualism and stasis as the principal alternatives.

The morphological changes in *Kosmoceras* far exceeded those for the Pleistocene gastropod *Poecilozonites* (Gould 1969) and the Devonian trilobite *Phacops rana*: (Eldredge 1971, 1972) - the two prime examples of punctuated equilibrium used by Eldredge & Gould (1972), and on this basis Raup & Crick argued that new biological species of *Kosmoceras* did indeed form as a result of gradual phyletic change. However, the true course of evolution was not linear; rather there were many reversals and variations in rate of change - but they thought this was eminently reasonable in a changing environment.

Raup & Crick (1981, p.206) thought the most likely interpretation of the *Kosmoceras* data was that it represented what a species in stasis looks like when sufficient high resolution data are available, i.e. 'They fluctuate mildly in morphology, with no apparent direction' (Gould & Eldredge 1977, p.115). The observed changes could result either from the tracking of minor environmental fluctuations or from slow genetic drift that affected an array of genetically interconnected populations.

One of the most interesting points raised by Raup & Crick is they thought that if environmental change were more frequent and more chaotic, plots of morphology verses time would become more chaotic, perhaps approaching the appearance of a random walk. In other words, an organism that is tracking a rapidly and randomly changing environment will produce a time series that appears random.

Raup & Crick (1981, pp.213-214) concluded their re-interpretation: 'In spite of the fact that the *Kosmoceras* data provide a nearly ideal testing ground for studying the evolution of morphology in single fossil lineages, the results of the present analysis are equivocal. Although the many reversals of evolutionary direction and the many changes in evolutionary rate appear to rule out a starkly simple orthoselection interpretation (constant selection pressure leading to linear change in morphology with time), a truly definitive case cannot be made for any other single interpretative model'.

Brinkmann's conclusions on evolutionary jumps and sedimentary breaks were re-evaluated by Raup and Crick (1982). The interpretation of evolutionary jumps in relation to sedimentary breaks is generally considered to be the centrepiece of Brinkmann's work, describing a real phenomenon in the sense that morphological jumps are associated with sedimentary breaks more often than would be expected by chance. Raup & Crick agreed with Brinkmann that there is a statistical association between morphological jumps and sedimentary breaks. However these morphological jumps, occurring in more than one lineage at the same time, only suggest that they could be either associated with sedimentary breaks (gaps in the fossil record) or punctuational events. These morphological jumps are compared directly with the bivalve data collected for this study (Section 7.11).

Brinkmann took measurements on the ammonites in the clay pits; the ammonites were then immediately discarded and certainly not retained for later examination. This is a problem as re-evaluations of Brinkmann's work (Raup & Crick 1981; 1982) are based entirely on Brinkmann's original identification, assignment to stratigraphic level, and measurements. My study on the same member of the Oxford Clay Formation has the bivalve specimens curated (at The Open University, see Appendix five for address) so that any

future work can study the original specimens collected, and not rely on someone else's data, as Raup & Crick had to do.

2.6.3 Relevant case studies supporting punctuated equilibrium

Since the work of Eldredge & Gould (1972) some sceptics have expressed views about the relevance of fossils in evolutionary theory. Some argue that the fossil record is just too sparse and incomplete to give an adequate account of phenotypic change. Schopf (1981) argued that molecular biology can tell us more about speciation events in the past than fossils ever can. Hallam (1982), however, said that to dismiss morphological criteria of species distinctions in favour of genetic ones, means getting rid of a large amount of data. He also said that we know next to nothing about the genetics of the vast majority of living species. Morphology remains an indispensable part of any comprehensive study of evolution (he also lists what he believes to be the requirements for adequate morphological testing - for full details see Hallam 1982, p.355). Hallam suggested that the Jurassic oyster *Gryphaea*, which has been a classic example utilised in evolutionary literature (Gould 1972), met the criteria admirably. The preservation of its thick calcite shells is excellent, they are highly visible, easy to collect and extremely abundant (found at many stratigraphic levels in countless millions, across five continents). In Hallam's earlier work (Hallam 1968, Hallam and Gould 1975) biometric analyses were undertaken on population samples collected from rich fossil horizons in Great Britain. The evidence, Hallam suggested, could be presented as either phyletic gradualism or punctuated equilibrium as the geographic control was inadequate. However, later Hallam (1982) analysed *Gryphaea* from a considerable geographic range: Great Britain, France, Germany, Switzerland, Austria, Hungary, Spain, Portugal, Israel, USA and Chile. He also looked at various museum collections (see Hallam 1982, p.355). In Hallam's earlier work (1968) the biometric study of *Gryphaea* samples from the British Lias concluded that there was significant changes up the stratigraphic succession which were independent of facies and hence attributable to evolution (see Hallam 1968 and 1982, pp.355-6). The further work of Hallam (see above localities) has revealed that changes first recognised in Britain can be traced across Europe as far as the Iberian Peninsula and Hungary. Thus there is no significant geographic

variation and the successive *Gryphaea* species have stratigraphic value to the precision of an ammonite zone or even subzone.

However, there is still the matter of whether they show phyletic gradualistic trends or punctuated evolutionary trends. Hallam's further collecting from the other countries illustrated that the morphological trends in the stratigraphic intervals between original samples indicated a pattern that was clearly not gradual but punctuational, with comparatively long periods of stasis intervening between the speciation events. One of the *Gryphaea* species, *gigantea*, lasted up to 14 million years in stasis. Hallam concluded his later work by saying that phyletic size increase is common in *Gryphaea* species, with a sharp initial increase, followed by longer periods of stability. No examples of phyletic gradualism were found. The widespread distribution of fossiliferous Jurassic strata across the world and excellent stratigraphic control (ammonite zonation) allowed recognition of evolutionary patterns, migration routes and centres of origin of particular species. Hallam (1982) also recognised a number of cases of allopatric speciation. He suggested that a strong relationship exists between physical environmental events inferred from facies analysis and the migration, evolution and extinction of *Gryphaea* species. It would have been interesting to compare the evolution of these *Gryphaea* with the environmental changes on a smaller scale (i.e. compared to the plus ça change model), to see if this was a real phenomena. More recent work, especially by Johnson, on *Gryphaea* is discussed in Section 2.6.4.

Punctuated equilibrium is illustrated by a Neogene cheilostome bryozoan called *Metrarabdotos* (Cheetham 1987). Within this genus nine species showed a pattern of stasis in overall morphology. The small number of unit character changes (changes in the mean values of a single-character within one species) that did show temporal trends within the *Metrarabdotos* species were interpreted statistically by Cheetham as chance deviations from the overall static pattern. He found no evidence that any single character trends in *Metrarabdotos* were sufficient to modify the punctuated pattern in overall morphology which characterised the nine species (Cheetham 1987, Figure 1, p.288). Other cheilostomes, studied by Jackson & Cheetham (1990) showed that three genera indicated a pattern of stasis punctuated by relatively sudden appearances of new morphospecies.

Cheetham & Jackson (1995) reviewed the phenotypic evolution of the two Tertiary-to-Recent genera of cheilostome bryozoans, *Metrarabdotos* and *Stylopoma*, and explored their possible modes of speciation. *Metrarabdotos* is one of the taxa which has showed the most persuasive evidence for punctuated speciation (Gould 1991). The less detailed record of *Stylopoma* appears to conform to the same pattern (Jackson & Cheetham 1994). Cheetham & Jackson (1995) tested for the evolutionary mechanisms underlying these patterns, based on quantitative genetic theory. These tests revealed that long-term evolutionary rates in these cheilostomes are too slow to have resulted from random genetic change (mutation and drift) alone. Thus Cheetham & Jackson (1995, p.204) concluded that 'evolutionary change must be concentrated within brief episodes of cladogenesis, consistent with the abrupt appearances of species in the record and with the basic tenet of punctuated equilibria theory associating evolutionary change with speciation'.

Stanley and Yang (1987) calculated rates of evolution for 19 lineages of Neogene bivalve over time intervals ranging from 1-17 Ma. They based the morphometric comparisons on 24 variables, for which more than 43,000 individual measurements were taken. They initially assessed evolutionary changes in shape for 19 early Pliocene (4 Ma old) species of bivalves by comparing these forms to their closest living relatives. To make their study unbiased and comprehensive, they included all species that met certain predetermined guidelines and that offered suitable fossil material for measurements. They then compared early Pliocene and Recent populations using: (1) all 24 variables treated separately; (2) multivariate distance (Mahalanobis' D), based on the full set of variables; (3) eigenshapes for shell outlines. They calculated net rates of evolution separating pairs of populations that belong to single lineages. For all intervals of time, the distribution of differences between population means for individual variables was remarkably similar to pairs of conspecific Recent populations from separate geographic regions. They analysed three different fossil species populations that were 17 Ma old and found that they resembled living populations almost as closely as geographically separated conspecific living populations today resemble each other.

Stanley & Yang suggested that if phyletic evolution is typically sluggish with respect to rates of large-scale evolution - for example, rates entailed in the origins of higher taxa - then we *must* look to speciation (phylogenetic branching) to account for most evolutionary change. They document a pervasive pattern of stasis for the morphology of burrowing marine bivalves during Neogene time, while not denying a very minor amount of net phyletic evolution. Stanley & Yang (1987, p.138) stated that high rates of size evolution for marine invertebrates have been reported, but they found shape experiences evolutionary stability. They therefore suggested that shape and size should be kept separate and disentangled in calculation of rates of evolution. Their results show only very minor net evolutionary changes in shape over 10^6 - 10^7 generations.

This study has disentangled shape and size changes in order to detect genuine morphological changes.

Lieberman *et al.* (1995) took more than 5000 measurements on over 1000 specimens of two species of brachiopod, *Mediospirifer audaculus* and *Athyris spiriferoides*, from the Middle Devonian Hamilton Group of New York State. Lieberman *et al.* (1995, p.22) concentrated on morphological changes through time within palaeoenvironments/biofacies, and concluded that samples from the first and last occurrences of the two species, from the lowermost and uppermost stratigraphical horizons of the Hamilton Group showed considerable morphological overlap. Some changes in morphology within the Hamilton Group were reversible and therefore count as evolutionarily significant changes and support the hypothesis of stasis sensu Lande (1986) and Gould & Eldredge (1977).

This study by Lieberman *et al.* is very significant because it shows how invertebrate evolution is affected by the palaeoenvironment/biofacies they live in. Here the results show overall stasis (across the 5 Ma period); however, the brachiopods evolved more in certain biofacies than others. The greatest morphological changes were recorded between samples from the lowest and intermediate stages of the Hamilton Group. This study takes this work into account, but goes one stage further and defines each biofacies, and whether it represents more stable or fluctuating environmental conditions (Chapter 6).

The Hamilton Group has been studied by other authors including Brett & Baird (1992; 1995) who suggested a co-ordinated stasis model for the shallow shelf Devonian fauna (Section 2.6.5).

A case that Gould & Eldredge (1993) used to support punctuated equilibrium is that of Williamson's (1981) mollusc lineages from a Cenozoic sequence in North Kenya. Williamson made three main points: (1) all lineages exhibit morphological stasis for very long periods of time (3-5 million years); (2) evolutionary change in each lineage is concentrated in relatively rapid speciation events (occurring over 5,000 to 50,000 years); and (3) the speciation events are accompanied by pronounced developmental instability in the transitional populations. Williamson suggested that all the lineages conformed to the punctuated equilibrium model with no cases of gradualistic trends occurring. He found long-term stasis in all lineages from both sexual and asexual organisms (see Williamson 1981, Figure 4, p.293). However, this study has been much criticised (e.g. Kat & Davis 1983 and Erwin & Anstey 1995), and is now considered not to hold up as a case of punctuated equilibrium, as it may well be attributable to ecophenotypic responses.

2.6.4 Relevant case studies supporting phyletic gradualism

Malmgren *et al.* (1983) tried to detect evolutionary patterns in the Late Neogene planktonic foraminifera *Globorotalia tumida*. The *G. tumida* lineage plays an important role in the zonation of the Upper Miocene-basal Pliocene tropical marine sequences, and was thus considered an ideal lineage to study evolutionary patterns. The mean morphotype changed gradually from *G. plesiotumida* to *G. tumida*, but reversals in direction were shown. The patterns could even be described as a random walk (Malmgren *et al.* 1983, p.382). However, there were periods within the lineage that exhibited relative stability (5 Ma), which were separated with the transition between *G. plesiotumida* and *G. tumida*. The data showed no splitting in the *G. tumida* lineage. Consequently, Malmgren *et al.* (1983, p.387) saw no evidence of either gradualistic or punctuated evolution in the *G. tumida* lineage, and proposed the term 'punctuated anagenesis' (originally termed punctuated gradualism) as 'an evolutionary pattern.... in which a lineage is more or less in stasis for long

periods of time, but in which these periods are punctuated by relatively rapid gradual change without lineage splitting'.

Re-examinations of these samples by Macleod (1991) were consistent with the punctuated anagenetic model as defined by Malmgren *et al.* (1983). However, Macleod also thought that the model did not accurately characterise the tempo and mode of evolutionary change of either the test-size or test-shape data, and thought the original chronostratigraphic interpretation of the sediments by Malmgren *et al.* (1983) was invalid. Thus Macleod's main purpose in his re-study was to point out the extent to which palaeobiological investigations depend fundamentally on sound stratigraphic analysis. The morphological transition from *G. plesiotumida* to *G. tumida* occurred within an interval of condensed sediment accumulation, consequently Macleod suggested the transition between these two planktic foraminiferal species should have been regarded as having taken place along a gradualistic continuum, but punctuated anagenesis remains a viable conceptual model for these data.

Over 15,000 trilobites were collected by Sheldon (1987) from an Ordovician sequence spanning a period of about 2 million years, from the Builth Inlier, central Wales. Over this period as many as eight trilobite lineages underwent a net increase in the number of pygidial ribs. Reversible shifts were found to be common, although the actual mean of ribs remained within fairly close limits in each section (Figure 2.5). Sheldon suggested that many trends driven by natural selection may be indistinguishable from random walks; however he believed that because all eight trilobite lineages showed the same *net* trend it strengthened the argument that selection was involved. Sheldon (1987, pp.562-563) said 'if change in rib number was only an ecophenotypic phenomenon one would expect far closer parallelism between lineages, as is clearly the case in size'. He suggested that the finding of gradualism in benthic macro-organisms such as the Builth trilobites is perhaps not surprising, given their setting. The Teretiusculus and Gracilis Shales accumulated in persistent low-energy dysaerobic conditions, probably in a silled marine basin several hundred metres deep. The shelly benthos is almost entirely restricted to trilobites, which flourished in this stable environment for several million years.' Sheldon (1987, p.563) suggested that 'perhaps this kind of gradual

phyletic evolution can only be sustained by organisms living in or able to track narrowly-fluctuating, slowly changing environments, whereas stasis, almost paradoxically, tends to prevail in more widely-fluctuating, rapidly-changing environments.' This was the basis to his later plus ça change model (Sheldon 1996b) (see Section 2.2.2).

When Sheldon's (1987) trilobite data were first published the debate about evolutionary patterns had been raging for 15 years. Eldredge and Gould have been quoted by Sheldon (1988, p.52) as saying 'let's concentrate on what we do find in the fossil record, not just on what we expect to find if only we had a good enough diary. What do we actually see? Answer: a new species appear suddenly - an abrupt punctuation - and then persists with little or no change - in equilibrium - before becoming extinct. We just don't see a gradual transformation from one species into another, however hard we look'. Sheldon found it impossible to identify the trilobites, and give them their specific names. There proved to be too many 'missing links' no longer missing, and intermediate rocks yielded intermediate specimens. Sheldon abandoned trying to identify species and concentrated on the detailed patterns emerging. The results showed a remarkable phyletic gradualism pattern of net increase in pygidial ribs. Sheldon (1988, p.54) said 'Through all the hype about punctuated equilibrium, Darwin's ideas have ridden the storm and emerged stronger than ever, but the detail of the evolutionary process remain something of a mystery.'

Sheldon's work is paramount to this study, illustrating how comprehensive collecting and sampling can reveal a gradualistic pattern where data might otherwise have been interpreted as evidence of stasis. Sheldon's work was probably one of the largest microevolutionary studies ever attempted, in terms of the numbers of specimens collected from numerous lineages. Sheldon also suggested that the gradualistic pattern detected was a response to the relatively stable environment in which the trilobites were living. This study attempts to take the study of Sheldon one stage further by detecting patterns from both stable and fluctuating environments, with a comprehensive collection of bivalves from more than one lineage.

In Section 2.6.3 *Gryphaea* was discussed as an example of the punctuated equilibrium pattern, as revealed by Hallam (1982). However, Sylvester-Bradley

(1977) considered the genus to provide good evidence of phyletic gradualism. Johnson & Lennon (1990) assessed Sylvester-Bradley's views and analysed over 15,000 specimens assembled by Sylvester-Bradley and obtained from their own field localities. Their main aim was to look at the two schemes; Hallam's model (1982) and Sylvester-Bradley's model (1977) which differ for the ancestry of the subgenus *Bilobissa* from *Catinula*. Sylvester-Bradley (1977, pp.59-60) considered that the Bathonian-early Callovian lineage, *Catinula*, was made up of a succession of forms in which four gradual trends are developed:

1. the genus increases in size;
2. the ribbing gets coarser and less distinct, and in later forms is restricted to early growth stages, or is absent altogether;
3. the left valve deepens so that there is an increase in the angle between the first growth line and the last;
4. a minor but increasing proportion of specimens develop a posterior radial sulcus.

These trends were said to effect a link with *Bilobissa*. In contrast, Brannan (1983, p.292), suggested that 'no strong trends either towards or away from gryphaeate or any other type of morphologies exist in the phylogeny of *Catinula*'. However, Brannan's investigation was based on a much smaller sample than Sylvester-Bradley's and therefore Johnson & Lennon (1990, p.459) suggested that it did not constitute an adequate test. They therefore decided to undertake an evaluation of the alleged traits and proposed that:

1. any demonstration of gradual transitions would place the iterative interpretation of *Bilobissa* evolution on at least as credible a footing as hypotheses of monophyly involving unaccountable stratigraphic gaps;
2. Sylvester-Bradley's criterion for recognising gradual evolution is as valid as Brannan's.

Principle measurements taken by Sylvester-Bradley were re-measured by Johnson & Lennon who investigated: length/periphery and height/length ratios, the direction of the transverse component of coiling, and the height and length of the attachment area in order to identify any possible morphological discontinuities or further gradual trends.

Brannan (1983) suggested that there was no evidence for gradualistic links between *Catinula* and *Bilobissa*. Johnson & Lennon suggested that there

was no compelling evidence for the existence of a morphological discontinuity between the Lower Callovian oysters, *Bilobissa* and Bathonian-Lower Callovian forms, *Catinula*. They also suggested that the existence of a gradual, unidirectional trend towards reduced frequency of ribbed morphs, together with somewhat less uniform trends in maximum size, coarseness of ribbing and peripheral height of the ribbed zone, provide positive evidence that Lower Callovian *Bilobissa* evolved from *Catinula*. They also suggested that the conclusion is strongly supported by close similarities in gross adult shell proportions, despite differing adult sizes.

Toarcian and Aalenian forms were analysed in the same manner (Johnson & Lennon 1990, pp.469-476), and it was noted that both the Toarcian-Aalenian and Bathonian-early Callovian groups of *Catinula* and *Bilobissa* have geometrically similar forms, despite differences in adult size.

Thus Johnson & Lennon felt they were justified in making the following conclusions (see Johnson & Lennon 1990, pp.469-476 for full details):

1. The subgenus *Bilobissa* was evolved iteratively (at least twice).
2. Callovian *Bilobissa* arose from a small ribbed, gryphaeate oyster *Catinula* by evolution over an interval of about 6 Ma (the duration of the Bathonian stage according to Harland *et al.* 1982). Change in single characters followed differing patterns - varying between unidirectional and at a steady rate, and oscillatory - but was never punctuational. Evolution between *Catinula* and Callovian *Bilobissa* can therefore be best described as gradualistic (*sensu* Sheldon 1987).

However, as we have seen evidence from Hallam (1982) (Section 2.6.3) suggested that the *Gryphaea* actually show a punctuated equilibrium pattern. From the data published up to 1990, it is extremely difficult to say for certain whether *Gryphaea* conform to either pattern.

New analysis of the existing data (Johnson 1993) suggested that the *Gryphaea* did not exclusively represent either punctuated equilibria or phyletic gradualism in pattern. Johnson found only a few cases where continuous evolution lasted more than one ammonite zone, but did find, within Jurassic scallops, good evidence of stasis lasting 5 Ma or more in as many as 34 species, and some evidence for stasis lasting 15 Ma or more. Johnson (1993, p.209) suggested that phylogeny involved significant intervals of both stasis and

more or less continuous evolution (although not representing classical gradualism), and that there remains much to be resolved about the details of *Gryphaea* evolution. He also suggested that further collecting and statistical analysis would be necessary for refinement of our understanding.

Johnson (1994) studied the Lower Jurassic *Gryphaea* (*Gryphaea*) species, and made further biometric studies of *Gryphaea* (*Gryphaea*) that were represented abundantly in the Lower Jurassic (Lias) of Europe. These were then compared to scallops, as these have frequently exhibited stasis over periods longer than 5 Ma and, like *Gryphaea*, scallop lineages often exhibit size increases. Johnson believed he could get an insight into the causes and controls of bivalve evolution by comparing the similarities and contrasts between the two.

In his earlier investigations, Johnson (1993) thought it possible that changes in individual shape characters for *G.* (*Gryphaea*) might be genuinely gradualistic. However, later he realised that assessment of this possibility required the construction of morphology/time plots. For these time plots Johnson assumed that the ammonite subzones are of equal duration, which is an unrealistic assumption and would have affected the pattern of results. Johnson (1994) included new data in this study and used ratios on peripheral height/length and peripheral height/height (Figure 4, p.176), and suggested the following:

1. The Lower Jurassic *G.* (*Gryphaea*) evolved by anagenesis without any significant intervals of stasis in all characters, or in shape characters alone. Individual characters seem to show brief intervals of stasis but otherwise may have undergone continuous evolution, admittedly with rate changes and reversals.
2. The overall rate of gross shape evolution in *G.* (*Gryphaea*) is probably a consequence of overall phyletic size increase.
3. The phyletic size increase shown by *G.* (*Gryphaea*) and many other Lower Jurassic bivalves probably represents an adaptation to stable, abundant food supplies.

Johnson & Lennon (1990) and Johnson (1993; 1994) unfortunately did not look at the changing physical environment of the Lower Jurassic sediments in detail. However, the Lower Jurassic *Gryphaea* correspond to

predictions of the plus ça change model (Section 2.2.2). From Johnson's (1994, p.185) conclusion 3 above, one could suggest that this phyletic size increase occurs when there is stable and abundant food supply, thus suggesting a relatively stable environment. Johnson & Lennon (1990, p.482) also suggested that more geochemical work was needed, as the small size of *G. (Catinula)* and of other bivalves is possibly due to large-scale environmental (? climate) changes during the Bathonian.

2.6.5 Some case studies supporting the plus ça change model

Brinkmann (1929) thought his ammonite evolutionary data showed a gradualistic pattern. However, probably the most important finding of Brinkmann's work was the evolutionary jumps in all the kosmoceratid lineages, for which he gave two explanations: 'they are either saltations (evolutionary spurts), or gaps in the record due to removal of sediment, and thereby of the fossils which would have been embedded in it. The latter explanation can be supported for the following reasons. Firstly, in no case does such a jump in kosmoceratid evolution occur in the homogeneous sediments (that is, strata of the same composition, i.e. the clays). Continuous sedimentation, then, is in all cases associated with constant evolution. Secondly the jumps occur not only in one lineage but in all branches of the genus *Kosmoceras*, simultaneously during the same sedimentary break' (p.68). According to the theory of the plus ça change model one would not expect to see any major evolutionary jumps within the homogeneous sediments, as this part of the section represents a more stable environment. The model proposes that stability in the environment leads to gradual, continuous morphological change, often with reversals, but overall giving a net change in morphology. The kosmoceratid lineages do show gradual net morphological change during this more stable period. The jumps in morphology occur at shell beds in all lineages simultaneously. Shell beds are known to be sedimentary breaks (Hudson & Martill 1994, Macquaker 1994, and Macquaker & Howell in press) and show a clear change in environmental conditions.

Cronin (1985) studied climatic fluctuations and their correspondence with evolution and speciation in marine ostracods. The formation of the Isthmus of Panama 3.0 to 4.0 million years ago changed ocean circulation and

the Earth's climate by ending the low latitude surface connection between the Atlantic and Pacific and increasing the northeastward flow of warm gulf stream water along eastern North America. This led to the growth of ice sheets on continents and high amplitude Pleistocene-type glacial-interglacial cycles now known from the deep-sea. During the climatic changes about 3.0 to 4.0 million years ago, directionless evolutionary stasis within lineages was seen. All six new species in the Pliocene first appear about 3.0 to 3.5 million years ago. Diversification of *Puriana* and other temperate and subtropical marine ostracode genera is causally linked with a climatic transition about 3.0 to 3.5 million years ago, thus suggesting that rather than causing mass extinction, as had been suggested for bivalves, this event actually disrupted long-term stasis, creating opportunities for rapid speciation. The plus ça change model predicts that if environmental fluctuations kick outside wide reflecting boundaries, one might expect to see a sudden evolutionary jump due to the change in environmental conditions. As the environment returns to within boundaries species tend to approximate to stasis (Figure 2.2a & b). The correlation of stasis with periods of cyclic climatic change indicates that marine ostracode species can tolerate cyclic sea-level oscillations such that some populations withstand severely diminished habitat resources, but can recolonise quickly when the habitat becomes available during the next sea level rise.

Parsons (1991, p.356), suggesting that stress has a great affect on long-term evolution, proposed that 'evolutionary change may therefore be most rapid in populations from habitats intermediate between these extremes [rapidly changing environments to nonstressful habitats], where there is some environmental stress associated with sufficient metabolic energy to allow some adaptive change'. Parsons (1991, p.357) agreed with palaeontological data from Sheldon (1987; 1990), and argued that 'maximum speciation rates are expected in habitats characterised by narrowly fluctuating environments, implying moderate stress, moderate genetic variability of ecologically important traits, and not unduly restrictive metabolic costs. In this way, gaps between palaeontology, physiology, ecology and evolutionary genetics are being bridged with the level of physical stress, especially climatic, being the connecting environmental link'.

Brett & Baird's (1992; 1995) studies of the Hamilton Group of New York State showed that it was possible to identify packages of rock, bounded in space and time, that contain coherent species assemblages that persist for millions of years in the face of physical and biotic disruptions. They suggested that these assemblages change rapidly and synchronously to a new stable composition over comparatively shorter time periods. Brett and Baird (1992; 1995) called this 'coordinated stasis' (see below). However, their study also supports the plus ça change model.

Morris *et al.* (1995) identified species in stasis for millions of years when there were physical and biotic disruptions, and rapid gradual change when the environment changed to more stable conditions. They claimed that the Hamilton Group data provided the best documented example of long-term faunal stability in the marine fossil record at the species level. According to Morris *et al.*, the disturbances indicate mainly changes in oxygenation.

Brett & Baird (1995, p.307) recognised 14 blocks of stability or coordinated stasis within one unit, and believed that the faunal associations or communities would have tracked a stable, but laterally shifting, environment. The communities appeared to be resilient to change even with the introduction of new taxa, and Brett & Baird (1995, p.308) believed this to indicate that these new organisms appear in great abundance only in a single cycle and then disappear abruptly, apparently within a period of no more than a few hundred thousand years. A strong relationship was demonstrated between turnover events and major transgressions with widespread anoxia. Six of the major faunal turnovers, including two boundaries in the Hamilton fauna, are closely associated with major sea level rise and deposition of black shales. There is also a possible association with climatic change in some cases. Evidence for global warming can be found at one event which terminated the Hamilton fauna. Thus they concluded (pp.308-309) that environmental shifts, probably involving changing water masses and related to sea level and/or fluctuations in climates, were responsible ultimately for undermining the stability of co-occurring species and were responsible for the large-scale punctuational patterns come to be seen throughout the fossil record. Sheldon (1996b) mentioned a written comm. from Brett (1995) that Brett and Baird's

findings are consistent with the plus ça change model and Sheldon's concept of stasis.

Jackson (1994, p.55) suggested 'most marine species appear abruptly in the fossil record and persist unchanged for millions of years.' Jackson reviewed evidence that communities of molluscs, reef corals and planktonic foraminifera had changed very little since the end of the Pliocene, approximately 2 Ma. Bivalve molluscs consistently exhibited morphological stasis during this time (Stanley and Yang 1987). This alone perhaps is compelling evidence for stasis in the seas. It has been suggested that the Quaternary upheavals are responsible for little evolution at present (Sheldon 1996b). Perhaps the upheavals of the Pleistocene were responsible for stasis predominating afterwards. Shifts in biota are due to major changes in climate, but once they occur, biotas persist more or less intact for millions of years despite repeated occurrences of the same climatic fluctuations. The Pleistocene cycles continued of low and high temperatures having little evolutionary effect because once through the initial thermal filter, all that was left were eurythermal species.

Analysis of Neogene and Recent benthic macrofauna communities by Stanton & Dodd (1994), in a wide range of habitats along the northeastern Pacific coast, provided the opportunity for the authors to separate the effects and relative magnitudes of environmental and evolutionary processes in unusual detail. The communities extend from the Late Miocene to the Recent (a 5 Ma time span). These communities exhibited 'a high level of stasis at the generic level', although they differed at the species level. However, during this time there were wide environmental fluctuations. The San Joaquin embayment was generally connected to the Pacific Ocean in the early Neogene; however, this connection became increasingly restricted during the Pliocene and Pleistocene.

The example of stasis within marine benthic communities in the Middle to Late Jurassic described by Tang and Bottjer (1995), previously considered as a study supporting the punctuated equilibrium model, is also a link to the plus ça change model. Tang and Bottjer showed an example of coordinated stasis within a fluctuating environment. During this period (20 Ma), four major marine transgressions occurred. However, Tang and Bottjer

described the palaeocommunity as being low-to-moderate diversity, with at times only 3 species making up 90% of the community. The plus ça change model (see Figure 2.2b) suggests that, along with predominant stasis in fluctuating environments, the diversity will also be restricted in comparison to a more stable environment. This is an excellent example of both low diversity and stasis.

Lazarus *et al.* (1995) investigated the speciation and evolution of *Globorotalia truncatulinoides*, a foram species from the mid-Pliocene. They found that it underwent its most rapid and extensive evolutionary change between approximately 2.5 and 2.8 Ma ago. This time interval corresponds to the development of northern hemisphere glaciation, suggesting that climate-controlled change may have influenced the evolution of *G. truncatulinoides*. (Numbers of specimens used in the study were greater than 2595 individuals, accompanied by wide geographical coverage). In the *G. truncatulinoides* lineage significant amounts of phyletic change were recorded during glaciation upheavals. However, during the last 1.5 million years, the foram exhibits stasis, during the time of widest climatic oscillations. This is especially true for the species *Globoconella inflata*, whose lineage from 1.73 to 0.25 million years ago suffered intense glacial/interglacial fluctuations.

Lazarus' work supports the plus ça change model (Section 2.2.2). Foraminifera were evolving during the beginning of the environmental fluctuations (onset of glaciation); however, after the glaciation upheavals, when the environmental conditions fluctuated most during the last 1.5 million years, stasis has prevailed.

2.7 'Real' evolutionary change ?

'Ecophenotypic effects are non-genetic (non-heritable) modifications of a phenotype that are produced in response to a particular habitat or environmental factor' (Sheldon 1993b, p.699). Ecophenotypy is an important limiting factor which must be considered when utilising fossils for microevolutionary studies, as there can be difficulty in distinguishing between genetic and non-genetic components of morphological change. 'Phenotypic divergence of local populations due solely to environmentally induced developmental changes (yielding distinct ecophenotypes), for example, might be erroneously interpreted as representing speciation' (Skelton 1993, p.465). An example of ecophenotypic variation would be house plants growing differently, depending on the different amount of light and water they receive. The problem within this current study is to deduce which are the ecophenotypic morphological changes against those genetically induced. This is an extremely large problem not just for this study but for all other evolutionary studies from the fossil record. Often the difference between ecophenotypes and genotypes cannot be recognised with certainty.

Within this chapter numerous case studies have been used as examples of microevolution in the fossil record. However, within a lot of these case studies ecophenotypic effects are not discussed. We must therefore question whether these are examples of 'real' evolution or just examples of ecophenotypic variation. Here ecophenotypy is discussed with direct relevance to this study.

Probably the only way to distinguish between ecophenotypic variation and true evolution is by utilising studies of 'Recent Environments'. Seed, over numerous years, has worked on the bivalve genus *Mytilus*, and specifically tried to determine species within the genus. Seed (1980, p.35) said that 'one of the most striking features of bivalve growth is the degree to which it varies with respect to age and environmental conditions.....numerous environmental factors, e.g. food supply, temperature, substratum, salinity, light, depth, turbidity, population density, and exposure to high-energy environments, are known to influence growth rate in bivalves.' Seed (1986; pers. comm 1997) studied two species of *Mytilus* (*M. edulis*, and *M.*

galloprovincialis) and found overwhelming evidence to suggest they are two separate species (through enzyme electrophoresis, DNA and artificial hybridisation); morphometric analyses alone could not determine two different species. Seed (1986, p.100) considered 'overall shell morphology in mytilids to exhibit considerable phenotypic variation; even mussels from different genera can appear superficially similar when grown under comparable environmental conditions. Such environmental control on shape (and growth) is readily demonstrated by transplanting mussels from one habitat to another'. Seed (pers. comm 1997) said that when he transplanted *M. edulis* to the environment where *M. galloprovincialis* lived, they grew and their shape (morphometrics) became extremely similar to *M. galloprovincialis* and vice versa. Seed (1992, p.125) even suggested that 'similar trends are exhibited by both *M. edulis* and *M. galloprovincialis* resulting in a considerable degree of convergence so that, in some populations shell characters merge until identification on gross morphology alone become difficult or impossible'. Seed (pers. comm. 1997) therefore suggested the only way to look for evolution would be to place both living species into identical environments where one can actually detect the selected characters.

Seed (pers. comm 1997) has studied *Mytilus* on a global scale (see Seed 1992, Figure 9, p.134), and seen an underlying trend in morphometrics and genetics and therefore is convinced that evolution into two separate species has occurred. He considers that globally environmental conditions show very large variations, and as a consequence of this it is impossible for environmental conditions to have had this effect on a genus. Evolution is the only possible mechanism.

Most previous evolutionary studies of bivalves from the fossil record have in general either not been able to deduce whether observed morphological changes are ecophenotypic variations or real genotypic variations, or have omitted to consider that the morphological changes could be ecophenotypic (e.g. Brinkmann 1929; Hallam 1975; Williamson 1981; Raup & Crick 1981, 1982; Macleod 1991). Many authors just simply assume that the significant shape changes found within the fauna are evolutionary.

Brinkmann (1929), who worked extensively on the *Kosmoceras* lineages from the Peterborough Member of the Oxford Clay (see Section 2.6.1 and 7.11

for further details), did not consider that the changes in the lineages could have been ecophenotypic. However, Brinkmann found a statistical association between breaks in succession (where major environmental changes occur) and jumps in morphology which could suggest an association between environmental changes and morphological changes. The morphological changes which occurred in all five lineages at the same time as major environmental changes occurred suggests environmental control on morphology, which could either be genotypic or ecophenotypic.

Williamson (1981) thought that his analysis of molluscs lineages from Cenozoic sediments in North Kenya represented evolutionary patterns conforming to the punctuated equilibrium model. However, this study is believed by many workers to show non-genetic morphological change attributed to environmental changes, i.e. the patterns are ecophenotypic and not evolutionary.

The examples above (see Section 2.6 for a complete discussion) are only meant to represent two examples of studies from the fossil record that have not taken into consideration the effects of the environment and therefore possible ecophenotypic variation. Some palaeontological studies such as that of Hallam (1982) have met the criteria (see Section 2.6.3) to use morphometric analysis to define species and evolution; Hallam studied *Gryphaea* globally and found similar trends in all species and ascribe the morphological changes to genotypic changes consistent with the punctuated equilibrium model.

Jackson & Cheetham (1990) were two of only a few palaeontologists to address the problem of cryptic variation, in closely-related species, or extensive variation in a single species suggesting spuriously that two are present. They suggested (p.579) that biological species may not be recognisable from morphology alone. 'A single morphologically defined species (morphospecies) might comprise two or more morphologically indistinguishable (cryptic) species or, alternatively several morphospecies might be defined from a single morphologically variable, interbreeding population. In either case, morphology would not be sufficient to discriminate species, and evolutionary stasis would be more apparent than real'. Jackson & Cheetham presented breeding experiments and protein electrophoresis experiments to discriminate biologic species of living Cheilostome bryozoa.

In the fossil record the problem of determining whether significant shape changes (true shape changes) are actually evolutionary changes (genetic change) or non-genetic environmentally induced (ecophenotypic) change can probably only be solved by looking on a global scale at the fossil species to be able to distinguish between real evolutionary change and ecophenotypic 'noise', or by comparing directly to a modern living relative. Seed (1986; 1992) has shown that environmental conditions do play a large part in determining the morphology of the shell of *Mytilus* at least. Within this study neither of these can be achieved. However, it is still possible to study the microevolutionary patterns from the bivalves of the Peterborough Member because statistical analysis can be carried out on the data obtained, determining how the shell grew (i.e. isometrically or allometrically, see Section 7.1), and sedimentological and geochemical analysis (see Chapter 6) can also determine the type of environment the shell grew in. These together give more of an insight into the mechanisms controlling the morphological changes.

Ecophenotypy is a huge problem for an palaeontologist studying evolutionary change. The problems are not unique to this type of study. Ecophenotypic variation is discussed (see Section 7.10) with direct relevance to the results obtained in this study and whether the microevolutionary changes can be considered 'real' microevolutionary changes or not.

2.8 Summary

Numerous other case studies exist to support both phyletic gradualism and punctuated equilibrium (see Erwin & Anstey 1995, pp.19-21). Only those particularly relevant to this study have been highlighted here. However, one can see from the cases briefly outlined above, much controversy still exists when placing an evolutionary pattern into a model. It appears almost impossible to place some patterns of evolution into either a gradualistic or punctuated model (Raup & Crick 1981, Malmgren *et al.* 1983, Johnson 1993). Previous studies have more recently been questioned, e.g. Raup & Cricks' (1981; 1982) re-evaluation of Brinkmann's (1929) work, Macleod's (1991) re-examination of Malmgren *et al.*'s (1983) work, and Johnson's (1993; 1994) re-investigations of Hallam's (1982) work. As Macleod (1991, p.183) said 'the importance of detailed quantitative analysis of morphological change in the

fossil record can hardly be overestimated.' This is true; although there are numerous cases of evolutionary patterns from the fossil record, more high resolution studies are needed. Erwin & Anstey (1995, p.11) said 'neither neobiologists nor palaeobiologists can usually 'see' speciation in action; both are left to infer what might have happened from a variety of indirect evidence'. From the list of evolutionary patterns given by Erwin & Anstey (1995, pp.19-21), a quarter of studies describing a single lineage display both gradual change and stasis. They also suggested (p.27) that caution was needed when interpreting gradualism and stasis as the evolutionary pattern, as varying sedimentary rates generate condensed and diluted intervals in succession that falsely appear as rapid gradualism and stasis. Other problems in detecting evolutionary patterns from the fossil record are described within Erwin & Anstey (1995, pp.27-28).

From these numerous examples, it is clear that the debate between punctuated equilibrium and phyletic gradualism has moved on, and it is no longer a case of either/or. Perhaps these two models just represent end points of a spectrum of evolutionary patterns (Figure 2.7) (Ridley 1996, p.562). The new plus ça change model attempts to integrate the punctuated equilibrium and phyletic gradualism models together. However, all three models should only be thought of as tendencies. There will never be a *definitive* model for evolution in the fossil record; it is far better to observe and examine the patterns emerging and their relationships to the changing physical environment, than try to 'box' them too soon into any specific model.

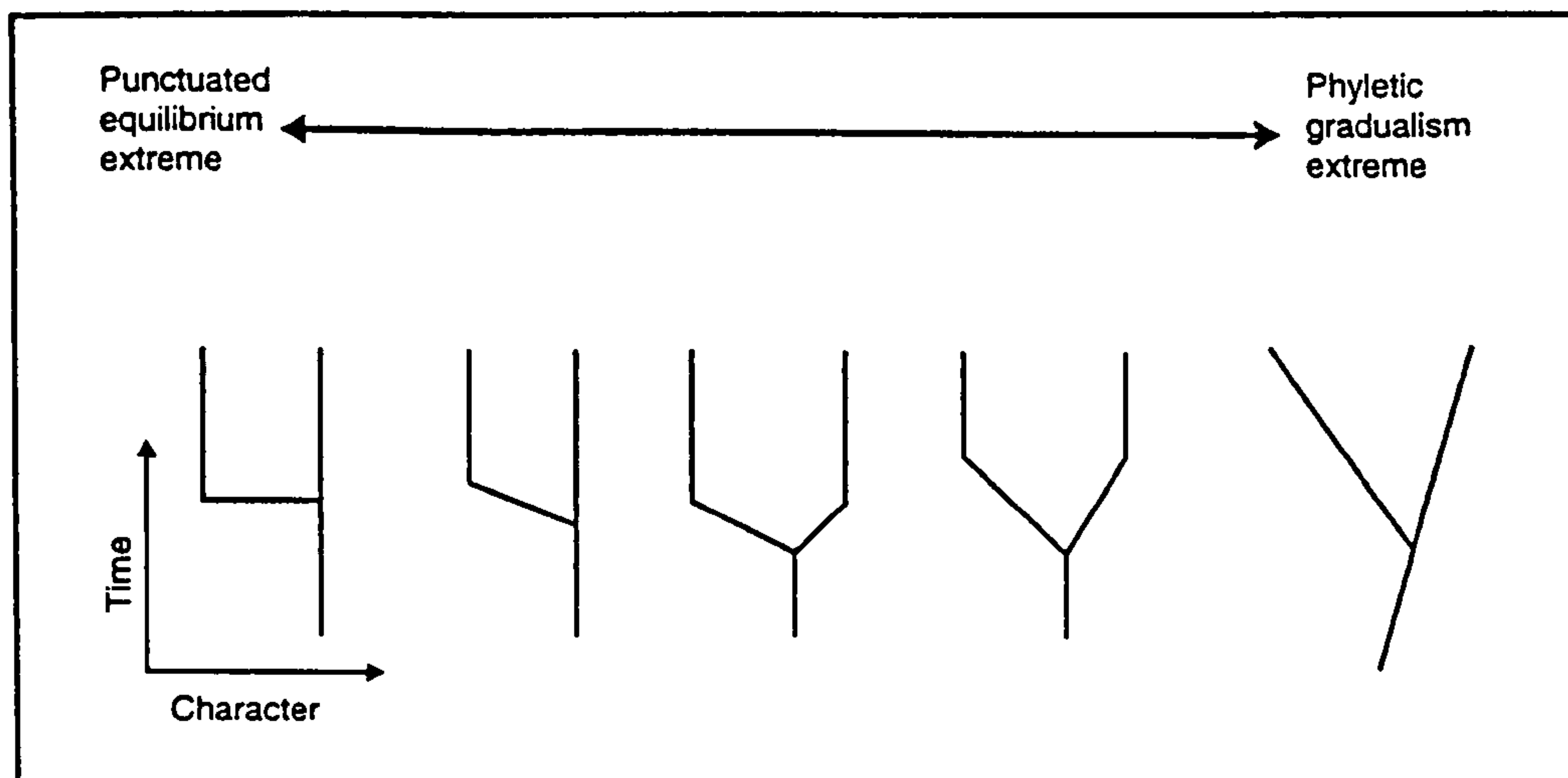


Figure 2.7. Spectrum of evolutionary models, from Ridley (1996, p.562).

CHAPTER 3

FIELD WORK AND CORRELATION

3.1 Aims of field work

The aim of the field work was to collect fossils from the Peterborough Member that could be measured accurately to produce data, which could be interpreted using statistical analyses to gain an insight into microevolutionary patterns. Although the material collected was mainly bivalves (see Figure 1.3), other macro fauna within the Peterborough Member was also collected. It was fundamentally important that collections were made with high stratigraphic resolution from sites with adequate exposures (see Section 1.1). Previous work published on the Oxford Clay Formation (Section 1.2) indicated that the most promising exposures of the Peterborough Member were within the brick pits and new landfill sites around Peterborough, Bedfordshire and Buckinghamshire.

3.2 Pit descriptions

3.2.1 Calvert landfill site, Buckinghamshire

Calvert landfill site is situated south west of Milton Keynes towards Aylesbury (Figure 1.1) (grid reference SP 695 232). The site was originally owned by the London Brick Company, which ceased production in the early 1990's. The site is now utilised as a landfill, operated by Shanks & McEwan Ltd. This recent abandonment of brick-making activities provides an ideal exposure of the Oxford Clay that is extensive and easily accessible. This pit was chosen as a collection site due to the vast continuous exposure and because access was made available courtesy of Shanks & McEwan Ltd. The site is composed of six pits, and a section was dug in pit 6 during the summer of 1995. This pit was not being landfilled at the time and therefore the section was preserved throughout the duration of the collection phase. A number of lagoons were present within the pit and these

inhibited access to some areas of the pit face in 1995. By 1996 the leachate from the landfill site had started to be pumped into the pit, and now (1997) the pit is dangerous and access extremely limited.

The south west facing wall of pit 6 (Figure 3.1) had the best exposure, comprising a face approximately 400-500 m long by 10-20 m high of relatively fresh clay. The floor of the pit is now at the base of the *obductum* Subzone (base of bed JC4), Figure 3.4 (in separate book of figures) and Table 1.1. The *obductum* Subzone is approximately 5 m thick, the *grossouvrei* Subzone above being approximately 4.5 m thick, with the boundary between the *obductum* and *grossouvrei* Subzones above the second well pronounced shell bed within the *obductum* Subzone. The *grossouvrei* Subzone extends to almost the top of the pit where only one bed of the *phaeinum* Subzone is exposed (bed JC12, 32 cm, see Figure 3.4).

Unfortunately the majority of the *jason* Subzone and the whole of the *medea* Subzone cannot be observed here as the landfill site requires a specific thickness of clay to act as a liner/seal around the waste, and thus it was not possible to dig deeper than 0.5 m into the *jason* Subzone, leaving well over 5 m of this subzone unstudied.

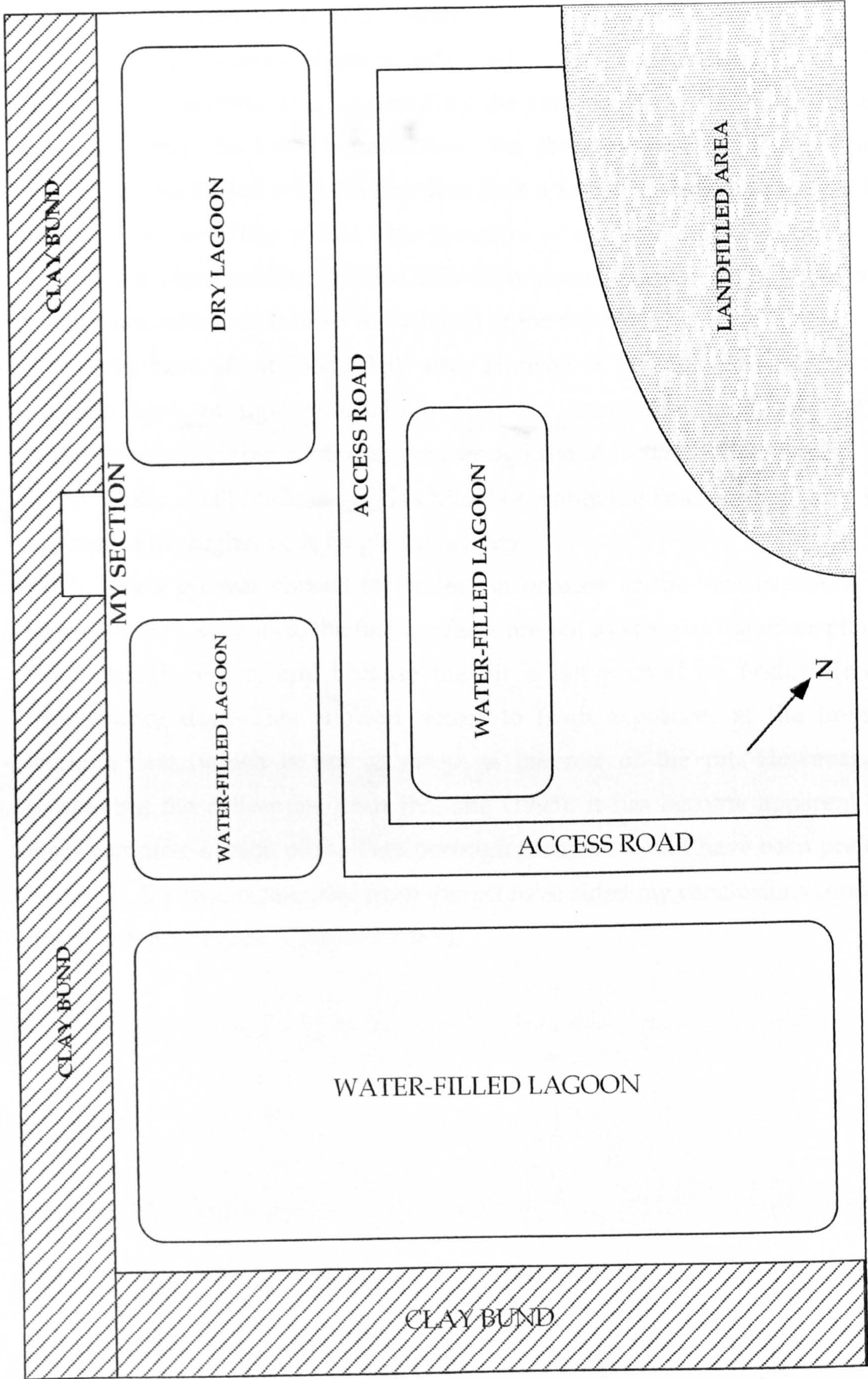


Figure 3.1. Sketch map of Calvert landfill site, Buckinghamshire.

3.2.2 Orton brick pit, Peterborough

Orton pit is situated just outside Yaxley near Peterborough Figure 1.1 (grid reference TL 160 940). It is operated by the Hanson Brick PLC, and is currently worked for clay for brick manufacture. The pit is excavated by 'drag line' and continually backfilled with overburden; thus a trench of approximately 1 km by 0.5 km is exposed (Figure 3.2). This produces a continual exposure for the whole of the 1 km, thus enabling detailed collection laterally; access to the upper parts of the face are, however, limited to each end of the exposure.

The base of pit (bed JO10, after Hudson & Martill 1994) (Figure 3.5, in separate book of figures) occurs within the *jason* Subzone. (Table 1.1). The Peterborough Member continues up through the *obductum* Subzone only. This is an unusually small thickness of this Member within the Peterborough area due to removal of the higher beds by glacial activity.

Orton pit was chosen for collection because of the vast exposure of the *jason-obductum* Subzones, the fact the faces are not as steep as the other pits in the Peterborough region, and because the pit is not worked on Fridays (machine maintenance day). This allowed access to fresh exposures at the immediate working face, which is not as steep as the rest of the pit. However, since completing the collections from this site (1995), it has become apparent that a more complete section of the Peterborough Member would have been preferable. However, the results obtained from this pit have aided my conclusions concerning the *obductum* Subzone (Chapters 7 & 8).



Figure 3.2. Photograph of Orton pit, Peterborough.

3.2.3 Saxon brick pit and King's Dyke brick pit, Whittlesey

Saxon brick pit (grid reference TL 248 965) and King's Dyke brick pit (grid reference TL 248 967) situated near to Peterborough, are currently working brick pits operated by Hanson Brick PLC. The two pits are separated only by the main road (A605) running from Peterborough to Whittlesey. Saxon and King's Dyke pits have been worked since the 1920's by a spectacular machine called a 'Shale Cutter' which rotates through an arc of 90° and cuts the clay from the face by a series of small blades which rotate round a chain and cut down the face, leaving it completely sheer (Figure 1.2).

Saxon pit provides an almost complete sequence of the Peterborough Member from the base of the *obductum* Subzone to the top of the *phaeinum* Subzone (see Figure 3.6, in separate book of figures). Unfortunately the pit is not worked down into the *jason* Subzone due to a layer of concretions which could cause damage to the shale planer; however, the *jason* Subzone can be exposed by a small amount of digging and is observed within drainage ditches.

Saxon pit was selected as a collection site, because a section of the Peterborough Member at Peterborough was required to compare with Calvert pit,

and more importantly, this pit has one of the best exposures of the Peterborough Member anywhere. Hudson & Martill (1994) provide a log of the section at King's Dyke pit (identical to Saxon pit), which was of great aid during the collection phase, and all these factors made it an ideal site. Saxon pit was chosen over King's Dyke pit for safety reasons due to engineering work which was being carried out in King's Dyke pit. The steep faces of Saxon pit produced by the shale cutter did cause a number of problems, and access was difficult at fresh faces and older slumped faces. During the early summer of 1996, the overburden (Stewartby Member) was being removed by a number of large mechanical excavators. Help was received from the manager, who allowed use of a mechanical excavator to dig out an old face and create a fresh 'stepped' exposure, therefore enabling even the higher beds to be reached (Figure 3.3).

3.2.4 Bletchley landfill site, Buckinghamshire

Bletchley landfill site was formerly a London Brick Company pit, and is now operated by Shanks and McEwan Ltd (grid reference SP 853 325). The pit is being filled with domestic waste, but will not be completely full for another 15 years. Within this pit good exposures of the *Acutistriatum* Bed are seen, which is a good marker horizon within the *phaeinum* Subzone. During initial collections at this pit it was noted that the exposures were extremely weathered and very difficult to access. Although the areas where collection was undertaken were not being utilised for waste disposal, the areas were being used for lagoons. Thus collections had to be made by standing on a steep slope adjacent to the lagoons. This was extremely dangerous and since the exposures were so weathered, this pit was not used as a main collection site.

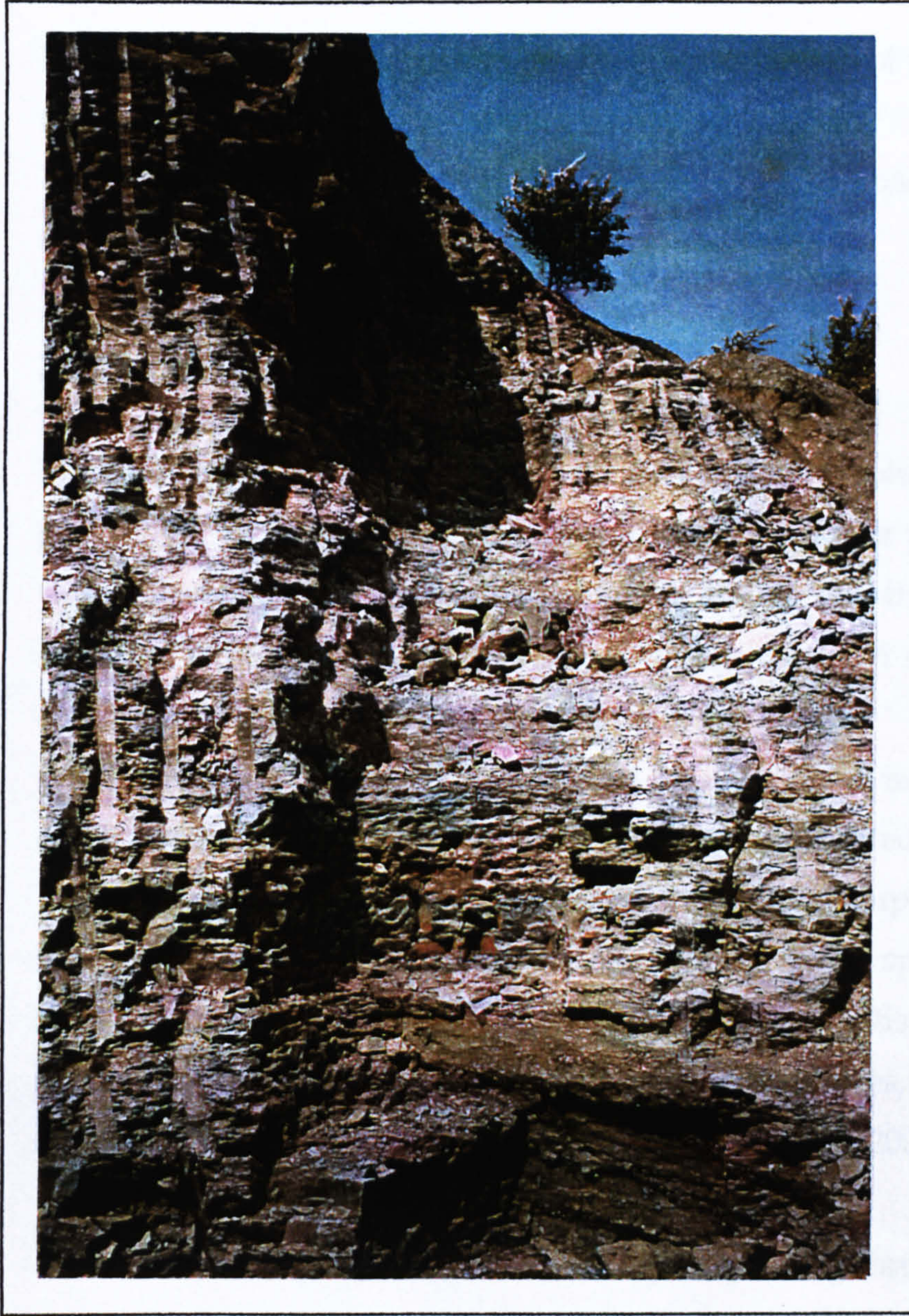


Figure 3.3. Photograph of Saxon pit, Peterborough.

3.2.5 Stewartby brick pit, Bedfordshire

Stewartby brick pit, Bedfordshire (grid reference SP 030 425), is an active brick pit operated by Hanson Brick PLC. The exposure in this pit is extensive, although fresh exposure is limited to the active face on one side of the pit. Exposure within this pit extends from the *jason* Subzone to the base of the *phaeinum* Subzone. Such a large exposure of Peterborough Member is now unusual to find in any of the working brick pits. In the Peterborough area the top of the *jason* Subzone is marked by a layer of concretions, which cannot be used in brick making and have to be extracted first. In general, the brick pits around

Peterborough are only worked down as far as the top of the *jason* Subzones so that these concretions do not have to be removed.

Stewartby brick pit was not collected from because of time restraints within this study.

3.3 Field methods

The initial aim of the study was to collect at high resolution from the three main pits (Calvert, Saxon and Orton pits) and to visit other pits for minor collections where necessary. However in the event, within the three main pits there was sufficient exposure such that extra collections were not required. The methods of collecting from the three locations are outlined below.

In order to test morphological change on a microevolutionary scale a continuous collection through a relatively uninterrupted sequence was required. For this study fauna was sampled continuously, grouping the fossils every 200 mm vertically. At every collection point a sample of 30 specimens was to be made, as this sample size was believed to be adequate for statistical analysis (Vines pers. comm. 1996). However, each bivalve has two valves, which can be different depending on the individual species, and thus over 200 specimens per 200 mm vertical interval required collection.

In fresh exposure, it was relatively easy to dig through the section from the top to the base; 200 mm was measured down on the face and a line at this level drawn accurately. The 200 mm thick slabs were dug out into large blocks using a spade and silage cutter, which were then chiselled open to reveal the fauna. The excess clay around the fauna was removed.

There were some serious problems with preservation of material during collecting, as the Oxford Clay is extremely soft and slightly moist; specimens tend to dry and crack up very easily, with loss of shell material. To avoid cracking and loss of shell a mix of PVA glue and water in the ratio of 50:50 was sprayed onto the clay. This penetrated into the clay and held the shell material together. This worked well with the initial samples, although there were a few problems with this over the summer of 1995 due to high temperatures ($>30^{\circ}\text{C}$), which caused the glue to evaporate and dry extremely quickly. There was a fine balance to be achieved between allowing the glue solution to dry sufficiently and preventing it

from lying in the sun too long and crack up. Two years on, none of the slabs have started to crack up and the glue solution appears to be holding extremely well. This technique is thus strongly recommended to other workers on clays.

3.4 Bed numbering

Previous workers who have studied the Oxford Clay (see Section 1.2) have included logs of all three localities utilised within this study (Callomon 1968, Duff 1974 and Hudson & Martill 1994). Although these workers did not concentrate on the high resolution stratigraphy of the pits, their logs were utilised. In order to provide continuity between these studies (and to avoid confusion) the bed-numbering system adopted for the localities is after Duff (1974) for Calvert and Orton pits, and Hudson & Martill (1994) in the case of Saxon pit.

The bed-numbering nomenclature adopted within this study after Duff (1974) and Hudson & Martill (1994) has been modified so that the bed numbers are preceded with two letters which indicate the pit, i.e. JC corresponds to Calvert pit, JS corresponds to Saxon pit and JO corresponds to Orton pit (J is for Jane). Therefore bed JS18, corresponds to bed 18 within Hudson & Martill's (1994, p.119) logged section at Saxon pit.

3.5 Correlation between sites

The main collection sites (Calvert, Saxon and Orton pits) have large geographical separation (over 70 km from Calvert to Saxon pits). Morphological patterns detected within the three pits need to be compared and therefore some form of correlatable evidence was required across the geographical area, e.g. refined biostratigraphy or excellent lithostratigraphic correlations.

3.5.1 Ammonite biostratigraphy

The Oxford Clay has been studied in detail since the late 19th century, but only relatively recently (Callomon 1968 and Page 1991) has an accurate ammonite biochronology been constructed. The scheme erected by Callomon (1968) can be used to correlate the Oxford Clay Formation across the East Midlands and beyond (Section 1.2.6). This scheme is based largely on the work of Arkell (1939), who

based his biochronology on previous authors studies and his own studies. The next section describes, in brief, the basis for the current ammonite biochronology.

3.5.1.1 Early zonation

Judd (1875) was the first person to work on the zonation of the Oxford Clay, but it was not until Neaverson (1925) published his work fifty years later that a provisional zonation was erected.

Neaverson (1925) noted that the zonal nomenclature for the English Upper Jurassic was incomplete. He published a table of the new ammonite zonations compared with Judd’s (1875) sequence:

Neaverson’s (1925) biozones	Judd’s stratigraphic sequence (1875)
<i>lamberti</i> <i>athleta</i> <i>duncani</i>	Dark-blue clays with pyritic ammonites
<i>castor</i>	Clays with <i>Belemnites hastatus</i> Clays with <i>Belemnites oweni</i>
<i>coronatum</i> <i>elizabethæ</i> <i>conlaxatum</i>	Clays with <i>Nucula nuda</i> and crushed ammonites

Table 3.1. Neaverson’s and Judd’s zonal scheme, after Neaverson (1925, p.29).

Arkell (1933, p.352) in a now classic work on the English Jurassic discussed the ammonite zonation of the Oxford Clay; he said of the zonation ‘the old records are too untrustworthy to base on them any conclusions as to the presence or absence of a separate zones of *renggeri* and *lamberti*, but modern evidence is forthcoming at Eye Green, Peterborough.’ He considered the paper by Neaverson (1925) to be valuable as it set forth a zonal classification. In the year following Neaverson’s seminal paper Brinkmann (1929) came from Germany to undertake a centimetre scale study of the evolution of the ammonite *Kosmoceras*. Arkell described the changes made by Brinkmann to Neaverson’s zonal table:

Brinkmann's Zonal modifications:	Corresponding Zone of Neaverson:
<i>Q. lamberti</i>	<i>lamberti</i> Zone
<i>K. spinosum</i> (= <i>orantum</i> Quenst.)	<i>athleta</i> Zone
<i>K. castor</i> and <i>pollux</i>	<i>duncani</i> <i>castor</i> <i>coronatum</i> <i>elizabethæ</i> Zones
<i>K. Jason</i>	<i>conlaxatum</i> Zone

Table 3.2. Brinkmann's and Neaverson's zonal scheme, after Arkell (1933, p.354).

However, Arkell said that although the zonation of Brinkmann was accurate 'we might as well be consistent and not overhaul our zonal scheme in order to introduce them [more zonal schemes] at Peterborough.' He suggested that the *elizabethæ* and *stutchburri* Zones should not be retained in name and that Buckmann's *conlaxatum* is a synonym of *jason*; he thus adopted the zonal table as follows:

Arkell's new zonal scheme	Equivalent of Brinkmann's/ Neaverson's zones
<i>C. præcordatum</i>	
<i>C. renggeri</i>	
<i>Q. lamberti</i>	
<i>P. athleta</i>	(= <i>spinosum</i> Zone of Brinkmann)
<i>K. duncanni</i>	
<i>E. reginaldi</i>	(= <i>coranatum</i> Zone of Buckmann and Neaverson)
<i>K. Jason</i>	(= <i>conlaxatum</i> and <i>elizabethæ</i> Zones of Neaverson, = <i>castor</i> and <i>pollux</i> and <i>jason</i> zones of Brinkmann)

Table 3.3. Arkell's zonal scheme, after Arkell (1933, pp.355-56).

Arkell (1939, pp.135-195) later made extensive collections of the ammonite fauna which he described in full. He used this new collection to re-think the

ammonite zonation of the Peterborough Member. Arkell had Neaverson send him ammonites which were collected from the *duncani* Zone. The assemblage was indistinguishable from that of the *proniae* Zone which Arkell studied at Wolvercote, Oxford. The dominant kosmocerate in both localities (forming at least 50% of the fauna) was *K. proniae*. Hence Arkell suggested that these all belonged to one zone. The name *proniae* Zone, Arkell thought, was appropriate as it is of much more recent origin, *duncanni* Zone being much older and often used by French authors in the wrong sense. Hence, Arkell adopted *Peltoceras athleta* to be the zonal index of both these beds, this being one of the oldest of all zonal indices, having been selected by D’Orbigny (1852, p.509) for part of his Callovian stage.

For the next zone below, the shales with *K. castor* and *K. pollux*, D’Orbigny selected another appropriate index, *Erymnoceras coronatum*. Reuter (1908) recorded that this species is restricted to this zone in Franconia, and it and allied species such as *E. reginaldi* are characteristic of the zone in the Peterborough district, Calvert (Buckinghamshire), Wiltshire, Dorset and France. Arkell (1939) decided that priority should be followed and *coronatum* is therefore used as zonal index. (It was previously adopted by Neaverson (1925) and Buckmann (1913, 1924-7) for finer local subdivisions included in what is now the present *coronatum* zone). For the basal zone Arkell suggested the use of d’Orbigny’s remaining index, *Kosmoceras jason*, which was used by universal consent.

Zone	Author first choosing zonal index and date	Important accessory fossils
<i>Peltoceras athleta</i>	d’Orbigny 1852; Oppel 1856-8	<i>Kosmoceras duncanni</i> , <i>K. proniae</i> , <i>K. transitionis</i>
<i>Erymnoceras coronatum</i>	d’Orbigny 1852	<i>K. castor</i> , <i>K. pollux</i> , <i>K. grossouvrei</i>
<i>Kosmoceras jason</i>	d’Orbigny 1852	<i>K. gulielmi</i> , <i>K. enodatum</i>

Table 3.4. Arkell’s revised zonal scheme, after Arkell (1939, p.213).

3.5.1.2 Refinements

Callomon’s (1955) examination of the ammonite fauna lead him to agree with Arkell that the species *E. coronatum* is, in fact, rare or absent in Britain, although he did find *E. reginaldi* and other species. Callomon therefore suggested the zonation be split into other subsidiary fossils - species of *Kosmoceras*. Previously *K. castor*

and *pollux* were chosen (Reuter 1908; Brinkmann 1929); however, they have long ranges and are therefore of little use. Callomon (1955) suggested a finer subdivision may be recognised on the basis of the equally common *Zugokosmoceras* - *Kosmoceras* (Z.) *obductum* (sparsely ribbed) in the lower part of the zone and *K. (Z.) grossouvrei* (densely ribbed) in the upper part of the zone. He confirmed, as according to Brinkmann (1929), that the two forms succeed each other and do not occur together. Callomon made a brief examination of the section at Calvert and he concluded that this was correct. However, examination of the same pit within this study shows that the two species do indeed overlap, and although they might not commonly occur in the same bed at the same time, they are not restricted to their subzone.

Callomon (1968, pp.280-289) provided stratigraphic logs for sections of the Peterborough Member, from numerous brick pits in the East Midlands region (Section 1.2.5). Callomon (1968, pp. 271-275) also described each ammonite zone and subzone, giving each diagnostic ammonite. This was the first time that the diagnostic features of all the ammonites from each zone had been described along with the new subzonal ammonites. The succession through the Peterborough Member was described by Callomon (1968) and is summarised below:

***S. calloviense* Zone:**

S. enodatum Subzone: A macroconch *Sigaloceras* (*Catasigaloceras*) *enodatum*, with short primary ribs.

***K. jason* Zone:**

K. medea Subzone: Diagnostic macroconchs *Kosmoceras* (*Gulielmites*) *medea*, like *S. enodatum*, but slightly larger (60-90 mm).

K. jason Subzone: Diagnostic macroconch *K. (Gulielmites) jason*, like *K. medea* but larger (100-130 mm) and ribbed to correspondingly later stages, although the body chamber is still smooth.

***E. coronatum* Zone:**

K. obductum Subzone: *K. (Zugokosmoceras) obductum* is the first of the macroconchs to retain some ornament to the end. It is smaller than *K. jason* (90-100 mm) and more involute and coarsely ribbed.

K. grossouvrei Subzone: *K. obductum* is succeeded by forms which are similarly and wholly ribbed but larger (130 mm) and more evolute. They are densely finely ribbed.

Peltoceras athleta Zone: This zone is the least well known because ammonites are much rarer, except at the base.

Callomon and Sykes (1980) discussed the ammonite zonation scheme, established by Callomon (1968), and made additions to the *athleta* Zone which they split into three subzones:

P. athleta Zone:

phaeinum Subzone - Index fossil: *Kosmoceras* (*Lobokosmoceras*) *phaeinum*.

proniae Subzone - Index fossil: *Kosmoceras* (*Lobokosmoceras*) *proniae*.

spinosum Subzone - Index Fossil: *Kosmoceras* (*Kosmoceras*) *spinosum*.

3.5.1.3 Latest developments

Callomon (1995, p.137) reviewed the Jurassic high-resolution geochronology, and said 'many fossil groups have been successfully used for high-resolution geochronology in the Jurassic, but almost always only as a substitute for ammonites when these fail.' The factors making ammonites such good guide fossils were listed in full by Callomon (1995, pp.137-138). In brief they are:

- An individual fossil, rich in morphological characters, conveys a lot of information. However, its potential as a guide-fossil really depends strongly on the taxonomic skill of the stratigrapher.
- Given the first reason, the number of specimens needed to characterise a stratigraphically diagnostic assemblage is relatively small. Typically, in ammonites, 5-10 specimens, if well preserved, should be sufficient to characterise a faunal horizon.
- The changes in morphology with time, which occurred for reasons still unknown, were much more rapid in ammonoids than any other group of invertebrates.

Page (1991, pp.15-19) summarised the ammonite zonal scheme of the Oxford Clay Formation. His work is a brief account of an unpublished work on the standard zones and subzones of the Oxford Clay. However, in order to keep this account succinct there was not so much detail in the published version compared to the unpublished version, which is currently the most clear and concise report on the zonation to date. The sequence of ammonite faunas characterising the zonal sequence and the defined boundary stratotypes for each subzone are summarised below (From Page pers. comm. 1996):

jason Zone

- Index fossil: *Kosmoceras (Gulielmiceras) jason* (Reinecke)
 Author: D'Orbigny, 1852
 Fauna: Corresponds to the range of *Kosmoceras (Gulielmiceras)*.

medea Subzone

- Index: *Kosmoceras (Buckman's) medea* (Callomon)
 Author: Callomon 1955
 Defined base: Base of bed 9, Peterborough Member, Kidlington, Oxford (Callomon 1955, Cox 1990)
 Fauna: *Kosmoceras medea* is typically abundant, and accompanied by occasional perisphinctids (*Homeroplanulites* or *Indosphinctes*), *Cadoceras* (C.) sp. and rare *Reineckeia* aff. *anceps* (Reinecke). A hectioceratid has also been recorded (Callomon 1968, p.282).
 Comment: Boundary stratotype was temporary exposure; replacement reference section needed.)

jason Subzone

- Index: *Kosmoceras (Gulielmiceras) jason* (Reinecke)
 Author: Callomon 1955
 Defined base: Base of bed 10, Peterborough Member, Peterborough (Callomon 1955, 1964, 1968, p.279; Hudson & Martill 1994, p. 118).
 Fauna: Dominated by *K. jason*, a larger species than *K. medea*. Other taxa are rare, and include *Indosphinctes patina* (Neumayr), *Cadoceras* (C.) *compressum* (Nikitin) and *Reineckeia* (R.) *anceps* (Reinecke).
 Comment: Boundary stratotype exists as an essentially temporary exposure in working and disused brickpits.

coronatum Zone:

- Index: *Erymnoceras coronatum* (Bruguière).
 Author: D'Orbigny 1852
 Fauna: Correlated using species of *Kosmoceras (Zugokosmoceras)*. *Erymnoceras* is locally common, mainly in the lower part of the zone.

obductum Subzone:

- Index: *Kosmoceras (Zugokosmoceras) obductum* (Buckman).
 Author: Buckman 1925, as a "hemera" (broadly similar to a chronostratigraphical horizon *sensu* Callomon 1985, p. 50; Callomon 1955, as a subzone).
 Defined base: Base of bed 14, Peterborough Member, Peterborough (Callomon 1964, 1968 p.279; Cox 1990, Fig 5; Hudson & Martill 1994, p. 118).

Fauna: The index is common, and accompanied by frequent *Erymnoceras coronatum*. Other taxa are rather rare, and include *Grossouvria* (G.) sp. and *Hectioceras* (?*Lunuloceras*) cf. *lugeoni* (de Tstovitch).

Comment: Boundary stratotype exist as essentially temporary exposures in working and disused brickpits. (The boundary does exist in a number of brickpits around Peterborough, and the management of Hanson Brick, Peterborough, are considering preserving a complete sequence of the Peterborough Member.)

grossouvrei Subzone:

Index: *Kosmoceras* (*Zugokosmoceras*) *grossouvrei* (Douvillé).

Author: Callomon 1955

Defined Base: Base of bed 17, Peterborough Member, Peterborough (Callomon 1955, 1968 p.279), Figure 5.

Fauna: Large species of *K.* (*Zugokosmoceras*) are typical; the lower part of the Subzone contains *K. (Z.) posterior* (Brinkmann), the upper part *K. (Z.) grossouvrei*. *Erymnoceras coronatum* is locally common in the lower part of the Subzone, but is replaced by rarer *E. argoviense* (Jeannet) at higher levels. Associated faunas are now richer, especially near the top of the Subzone, where *Binatisphinctes comptoni* (Pratt) is abundant and *Hectioceras* (*Sublunuloceras*) *lonsdali* (Pratt) common. Occasional *Grossouvria* (G.) cf. *leptoides* (Till) and rare (*C.*) *milashevici* (Nikitin) have been recorded from the lower part of the Subzone. Reineckeids are known very rarely and probably include *R. (Collotia)* sp.

Comment: 'Boundary stratotypes exist as essentially temporary exposures in working and disused brickpits.' (Again, like the Coronatum Subzone, this might now exist permanently.)

Upper Callovian Substage

athleta Zone:

Index: *Peltoceras* (P.) *athleta* (Phillips).

Author: D'Orbigny 1852, Oppel 1857.

Fauna: Detailed subdivision is made on the basis of species of *Kosmoceras* (*Lobokosmoceras*) and early *K. Kosmoceras*, all with looped ribbing (see taxonomy section). Peltoceratids are abundant at certain levels, mainly in the middle and upper parts of the zone.

phaeinum Subzone:

Index: *Kosmoceras* (*lobokosmoceras*) *phaeinum* (Buckman).

Author: Callomon and Sykes, 1980; = Lower Athleta Zone of Callomon (1964, 1968); equivalent, in part, to the *acutistriatum* Hemera of Buckman 1924.

- Fauna:** Dominated by *K. (L.) phaeinum*, with occasional *Binatisphinctes comptoni*, *Hecticoceras (Sublunuloceras) lonsdali* and rather rarer *Longaeviceras laminatum* (Buckmann) and *Reineckeia (Collotia) spathi*.
- Comment:** The boundary stratotype is in a working brickpit and is essentially a temporary exposure. Callomon & Sykes propose a Scottish reference section for the Subzone (shore Sutherland; Callomon & Sykes 1980, p.46). If the type-locality those authors propose at Calvert, Buckinghamshire is lost, the Scottish reference section may include a suitable replacement boundary stratotype.' (If a section at King's Dyke brickpit is preserved this may be more suitable for the replacement boundary stratotype; Callomon *et al.* 1989.)

3.5.1.4 Summary

Although ammonite subzones can be correlated between individual pits in the Peterborough area, correlating using the ammonite zonal scheme between Peterborough and Calvert Pit is more difficult (Callomon pers. comm. 1997). Although the ammonite subzonal level will be the same in each pit, the beds either side may not be the same due to: erosion, non-deposition and other factors which can cause major differences. Other methods of correlation between Peterborough and Calvert were therefore investigated for this study.

3.5.2 Correlation using shell bed horizons

At the start of the *phaeinum* Subzone a marker horizon, the *Acutistriatum* Bed, occurs. This bed, along with the *Comptoni* Bed (at the top of the *grossouvrei* Subzone), has long been recognised by its lithology and ammonites, and used in correlation from Dorset to Humberside (Hudson & Martill 1994). The *Acutistriatum* Bed can be used to correlate the top of Calvert pit (bed JC12) (Figure 3.4) with bed JS38 at Peterborough (Figure 3.6). However, this is only one bed at one correlatable place in the succession, and does not allow correlation of Orton pit with Calvert and Saxon pits.

After detailed examination of the succession within the numerous brick pits across the East Midlands region a similar pattern emerged - shell bed horizons appeared to occur at the same levels within numerous pits:

PIT SUB- ZONE	PETERBOROUGH		BEDFORDSHIRE	BUCKINGHAMSHIRE	
	SAXON	ORTON	STEWARTBY	BLETHCLEY	CALVERT
PHAEINUM	ACUTISTRIATUM BED				
GROSSOUVREI	SHELL BED		SHELL BED	SHELL BED	SHELL BED
	F. SHALE	S. CLAY	SHELL BED	B. SHALE	S. CLAY
OBDUCTUM	SHELL BED	SHELL BED	S. CLAY	SHELL BED	SHELL BED

Table 3.5. To illustrate that shell beds are present between the *obductum* and *grossouvrei* Subzonal boundary (F. Shale = fissile shale; S. Clay = shaley clay; B. Shale = bituminous shale).

Table 3.5 shows that at the boundary of the *obductum* and *grossouvrei* Subzones, in all except Stewartby pit, there appears a shell bed before the subzonal boundary. Examination of this shell bed in all locations (except Bletchley pit, as this is no longer exposed and therefore could not be examined) found the same fauna - a nukulacean shell bed, comprising *Palaeonucula* and *Mesosaccella*. The benthic fauna even matched across the region down to the species level (*M. morrisi*). However, correlation of microfauna requires further study. The formation of a shell bed requires significant changes in the environment (see Chapter 6), and

these significant environmental changes may be what drove *K. (Z.) obductum* to decline in numbers and *K. (Z.) grossouvrei* to evolve. Sedimentological data show that the silt:clay ratio across this subzonal boundary shows dramatic change from a silt-rich mudstone to a very coarse shell bed/coarse silty mudstone (at Saxon pit) (see Figure A4.1), also suggesting an environmental change (Macquaker & Howell in press).

It is probable that these shell beds correlate across the East Midlands region. The fact that they occur at the subzonal boundary in every pit across the region with the same faunal composition suggests that a distinct change in environment occurred at this time and that the shell beds are a result of that change.

3.5.2.1 Summary

Table 3.5 illustrates both the subzonal boundaries and the shell beds above and below them. Palaeontological and sedimentological studies of the shell beds (see Chapter 6) at the *obductum-grossouvrei* Subzones indicate identical macro faunal composition of the shell beds, dramatic change in the silt:clay ratio, and a change in every geochemical parameter discussed in Section 6.4. The morphological changes in the bivalves show that when the graphed results from Calvert pit and Saxon pit are overlain they correlate best when the shell bed horizons are matched up at the *obductum-grossouvrei* Subzonal boundary (see Figure 7.48). This piece of evidence is crucial; the morphological data obtained is of a very high resolution, and the change in environmental conditions across this Subzonal boundary can be identified by the matching data from both pits. Thus the shell beds at the *obductum-grossouvrei* Subzonal boundary, and the *Acutistriatum* Bed at the *grossouvrei-phaeinum* Subzonal boundary will be used for precise correlation in this study.

CHAPTER 4

THE LITHOFACIES AND BIOFACIES OF THE PETERBOROUGH MEMBER

4.1 Introduction

The Peterborough Member is predominantly a mudrock deposit within a largely argillaceous formation. Despite this dominance, numerous different and subtle lithological differences may be recognised. This chapter gives some descriptions of the different lithofacies previously recognised, which have been used within this study as background information for recognising the distinct environments of the Peterborough Member (see Chapter 6).

4.2 Facies recognised by Duff (1975)

Duff (1975) recognised five distinct lithologies or facies within the member: silts and silty clays; bituminous shales; shell beds; blocky claystones; and calcareous clays. Three out of the five facies were sampled within this study: bituminous shales; shell beds; and calcareous clays.

Furthermore Duff (1975) recognised seven, out of his ten, distinct biofacies within the Peterborough Member (Section 1.2.7): deposit-feeder bituminous shales; *Grammatodon*-rich bituminous shales; foraminifera-rich bituminous shales; nukulacean shell beds; *Grammatodon* shell beds; *Meleagrinella* shell beds; *Gryphaea* shell beds; all except the *Gryphaea* shell beds were sampled during this study.

4.2.1 Bituminous shale facies

This lithofacies comprises well-laminated or fissile shaly clays with a high organic carbon content (3.0 - 4.7%), and comprised the bulk of the Peterborough Member. Duff (1975) recognised three biofacies within this facies: deposit-feeder bituminous shales, *Grammatodon*-rich bituminous shales and foraminifera-rich bituminous shales.

4.2.1.1 Deposit-feeder bituminous shales (DFBS)

The major fraction of the Peterborough Member is of DFBS biofacies (beds, JC6, JC8, JC10A & JC10C, Calvert pit (Figure 3.4); beds JS14, JS15, JS16, JS18, JS24, JS26, JS28, JS34 & JS35, Saxon pit (Figure 3.6)) and is dominated by the so-called 'pendent' bivalves *Bositra* and *Meleagrinnella*, as well as deposit feeders such as *Procerithium*, *Dicroloma*, *Mesosaccella* and *Palaeonucula*. There is also a wide diversity of infaunal and epifaunal suspension-feeders, although these are less common (Duff 1978, p.16) (Figure 4.1).

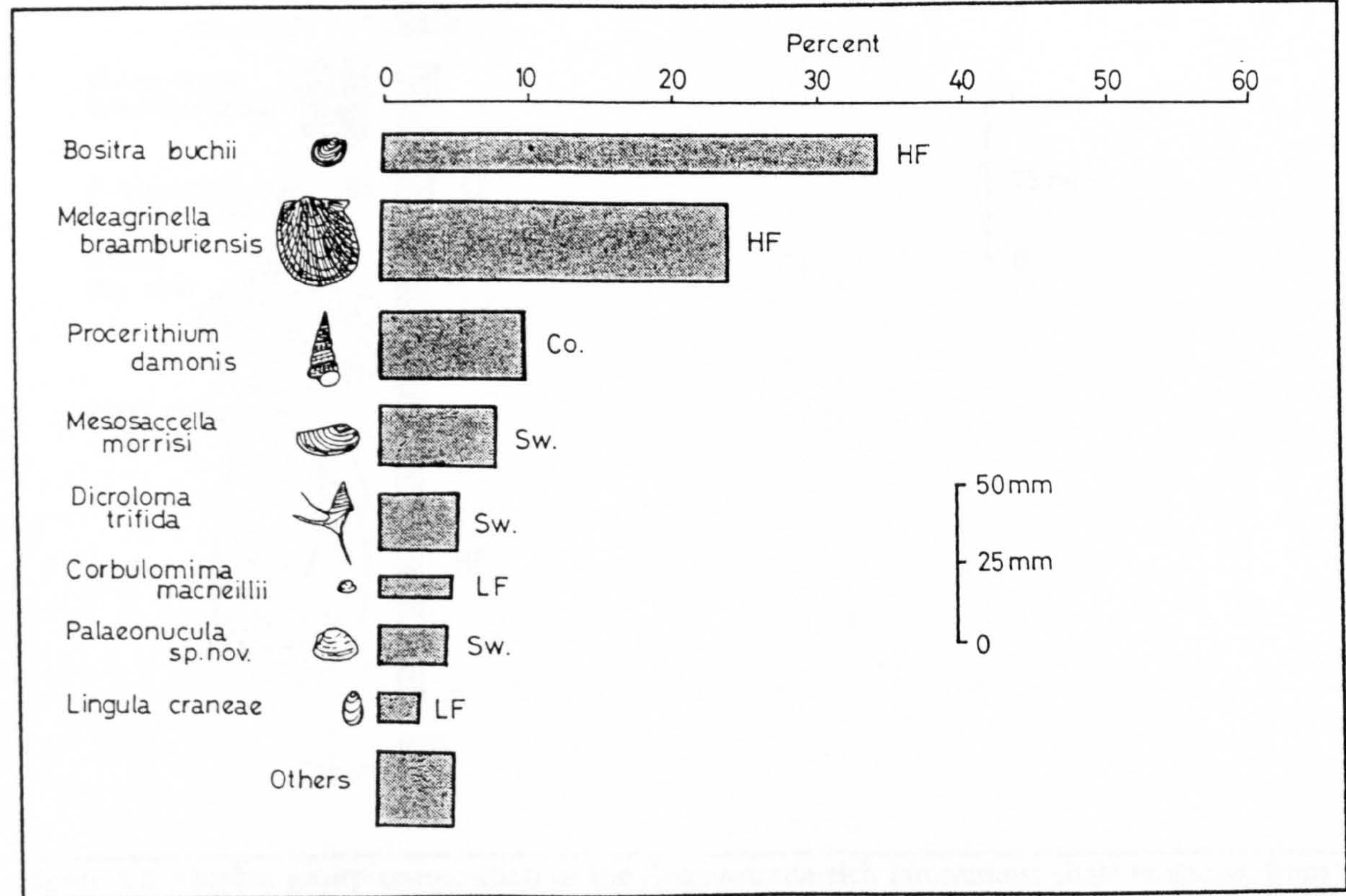


Figure 4.1. Trophic group composition of the deposit-feeder bituminous shale biofacies, from Duff (1975, p.463).

4.2.1.2 *Grammatodon* - rich bituminous shales (GRBS)

This is a bituminous shale biofacies which has fewer epifaunal suspension-feeding bivalves than the DFBS (Duff 1975). The dominant species are deposit-feeders (*Procerithium* and *Mesosaccella*) (Figure 4.2). Unlike the DFBS there was evidence for niche partitioning amongst the dominant species (bed JC9, Calvert pit and bed JS34, Saxon pit, Figures 3.4 & 3.6).

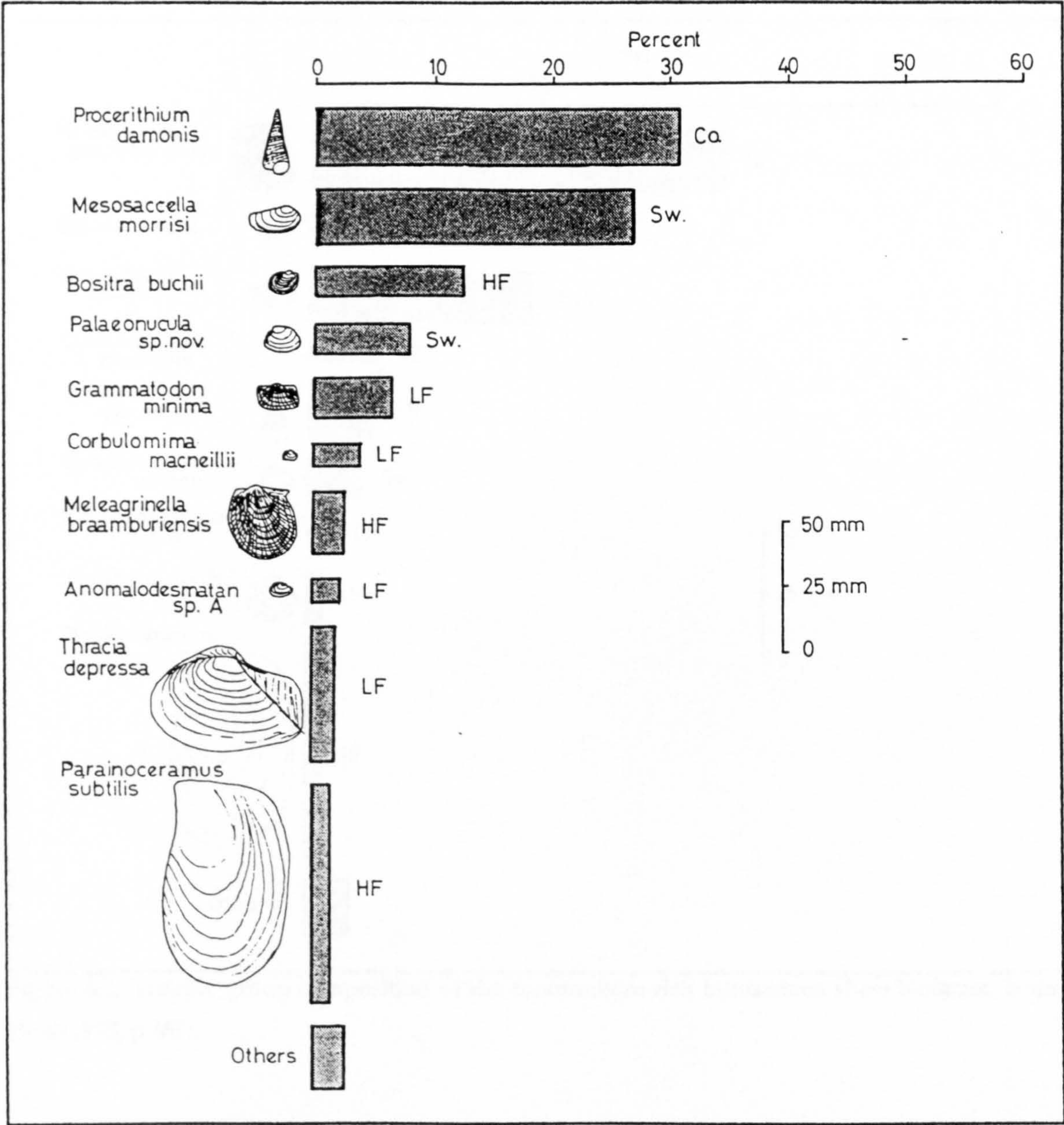


Figure 4.2. Trophic group composition of the *Grammatodon*-rich bituminous shale biofacies, from Duff (1975, p.466).

4.2.1.3 Foraminifera-rich bituminous shales (FRBS)

This biofacies contains abundant foraminifera in an otherwise normal bituminous shale. The trophic composition of the FRBS biofacies is also related to the DFBS and is also associated with the GRBS. Duff (1975) found the only way to distinguish between these three biofacies was by the presence of abundant foraminifera. Duff (1975) assigns his bed 4 of Calvert pit (JC4, Figure 3.4) to this facies (Figure 4.3).

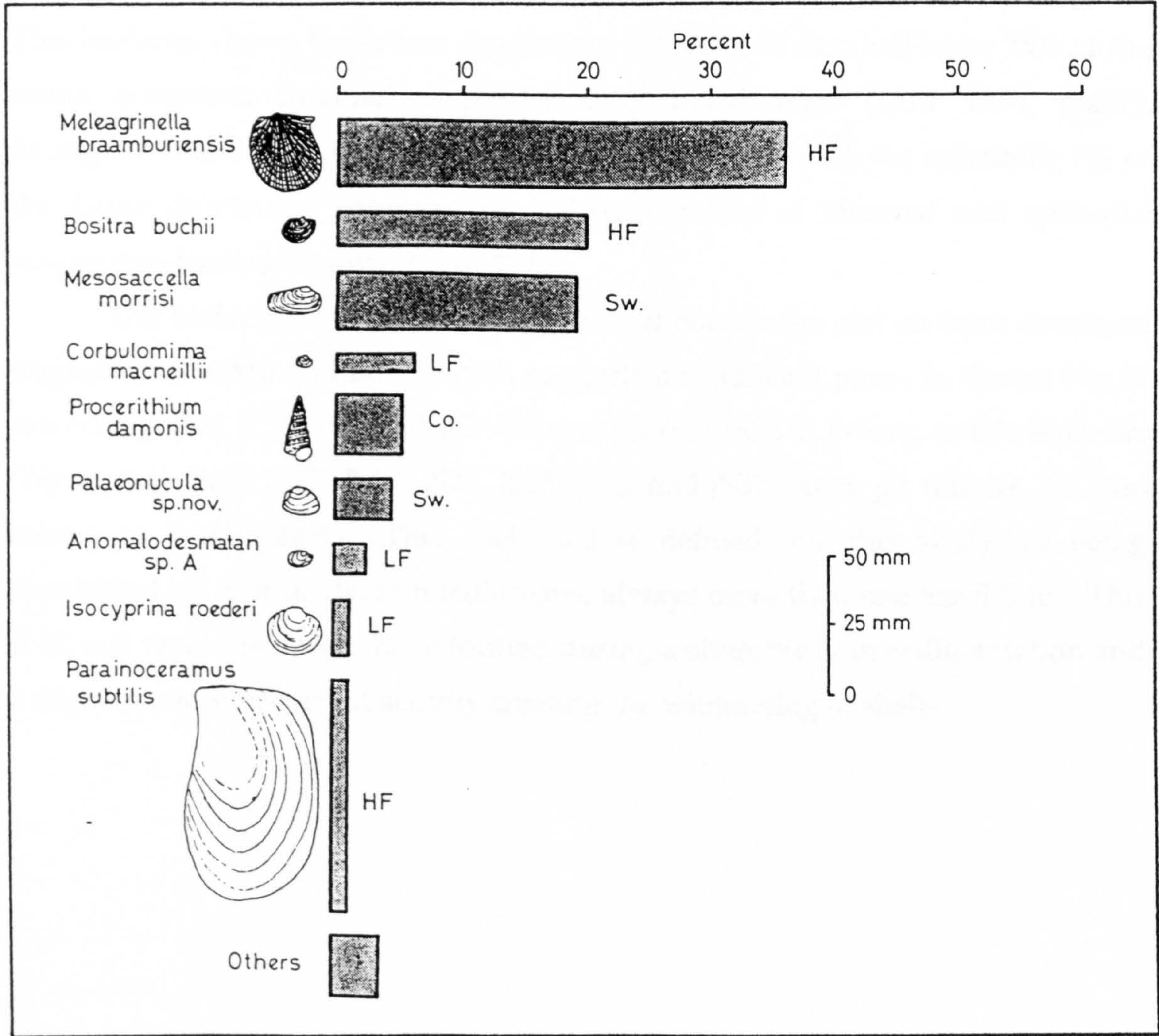


Figure 4.3. Trophic group composition of the foraminifera-rich bituminous shale biofacies, from Duff (1975, p.467).

4.2.2 Shell beds

Shell beds within the Oxford Clay Formation are normally relatively thin, with accumulation of shelly debris usually being little more than 200-300 mm. At least four very distinct shell beds have been recognised within the Peterborough Member: nukulacean shell beds; *Grammatodon* shell beds; *Meleagrinella* shell beds; and *Gryphaea* shell beds (Duff 1975). Only three were sampled within this study; the *Gryphaea* shell bed facies tend to be restricted to the lower part of the *jason* Subzone, and were not sampled.

4.2.2.1 Nukulacean shell bed (NSB)

This biofacies shows the lowest dominance diversity of the shell beds: 75% of the fauna comprises infaunal, deposit-feeding nukulaceans (Duff 1975, p.467). *Meleagrinella* and *Procerithium* together constitute 18.2%, with the remaining 7% of the fauna distributed between some fifteen species of infaunal and epifaunal suspension-feeding bivalves (Duff 1975).

This biofacies is often found at subzonal boundaries and contains abundant fragments of wood and bone which suggests a significant pause in deposition or reworking. Bed JC11, JC5 and JC7 Calvert pit (Figure 3.4) belong to this biofacies (Figure 4.4). Beds JS17, JS19, JS23, JS25, JS35 and JS37 Saxon pit (Figure 3.6) also belong to this biofacies. This shell bed is defined, for this study, as being dominated by disarticulated nukulaceans, always more than one fossil thick. This shell bed would probably have formed during a short break in sedimentation and a slight increase in current activity creating the winnowing of shells.

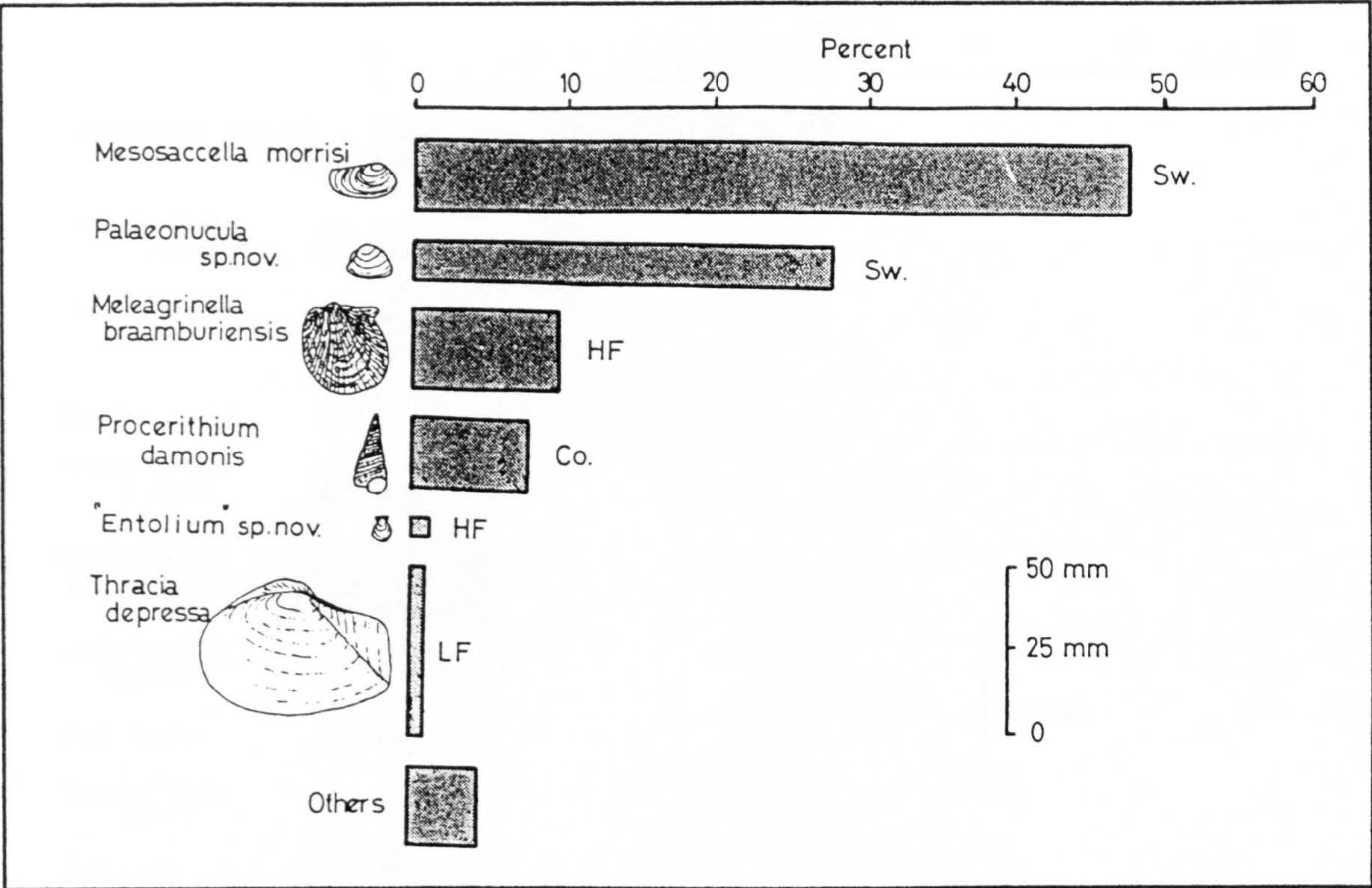


Figure 4.4. Trophic group composition of the nukulacean shell bed biofacies, from Duff (1975, p.468).

4.2.2.2 *Grammatodon* shell bed (GSB)

This biofacies occurs within the *Grammatodon*-rich bituminous shales and has a similar trophic group composition to the DFBS. Duff (1975, p.468) suggested that these shell beds are likely to have been formed by slower rates of sedimentation or a slight increase in current activity.

This biofacies occurs within parts of bed JC9 and JC10B, Calvert pit (Figure 3.4) and is always found to be more than one shell thick, with mainly disarticulated shells; they are also richer in *Mesosaccella* than any other deposit-feeder facies (Figure 4.5). This shell bed is defined, for this study, as being dominantly composed of *Mesosaccella* with *Grammatodon*.

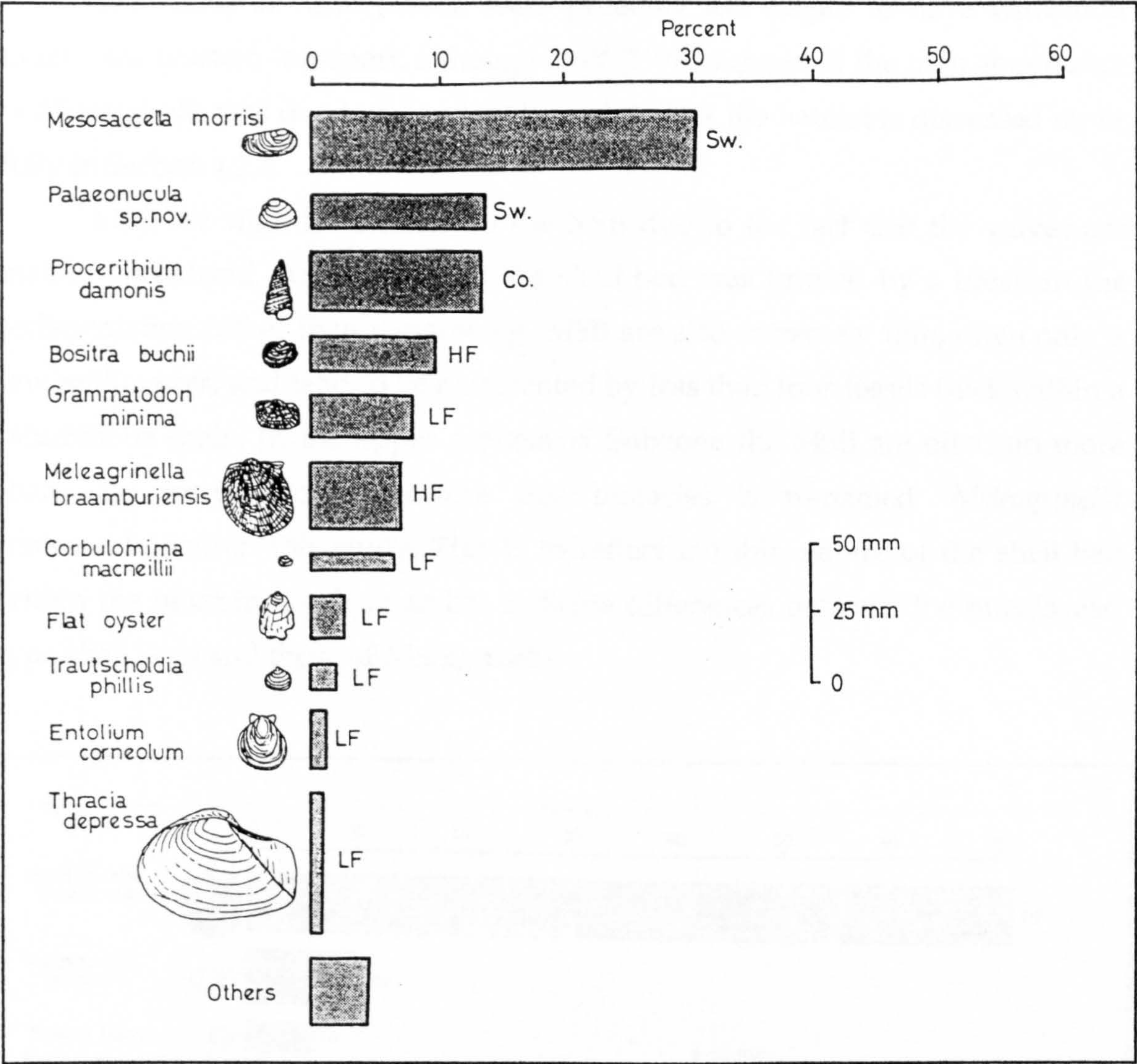


Figure 4.5. Trophic group composition of the *Grammatodon* shell bed biofacies, from Duff (1975, p.469).

4.2.2.3 *Meleagrinnella* shell bed (MSB)

Duff (1975, p.469) thought this biofacies was largely confined to the upper part of the *grossouvrei* Subzone, where the shell beds were interbedded with calcareous clays, and consisted overwhelmingly of a concentration of broken and unbroken specimens of *Meleagrinnella braamburiensis*. However, this study has found overwhelming evidence for the domination of *Meleagrinnella* within the *obductum* Subzone (see Figures 6.1a & b). Most of these shell beds are bounded above and below by burrowed surfaces, where fragments of the overlying bed are piped down into the bed beneath. Burrowed horizons are rare elsewhere within the Peterborough Member and these are thought to represent phases of slow or nil-deposition, with increased current activity (Duff 1975) (Figure 4.6).

The shells of *Meleagrinnella* were probably too fragile to have withstood much post-mortem transport, although Duff (1975) suggested the high abundance of *Meleagrinnella* was due to a pendent life habit. This life habitat is discussed more fully in Section 4.2.4.

MSB are slightly different to the NSB due to the fact that the valves are mainly articulated, suggesting that the shell bed was formed by a break in the sedimentation rather than winnowing. MSB are also extremely thin, often only a few millimetres, and tend to be represented by less than four fossils thick within a bituminous shale. In the upper *grossouvrei* Subzone the MSB are often no more than one fossil thick. Therefore this biofacies is re-named '*Meleagrinnella* pavements' within this study. This is to reflect the thin nature of the shell bed within the bituminous shale and to indicate differences between the nukulacean type shell beds and those of *Meleagrinnella*.

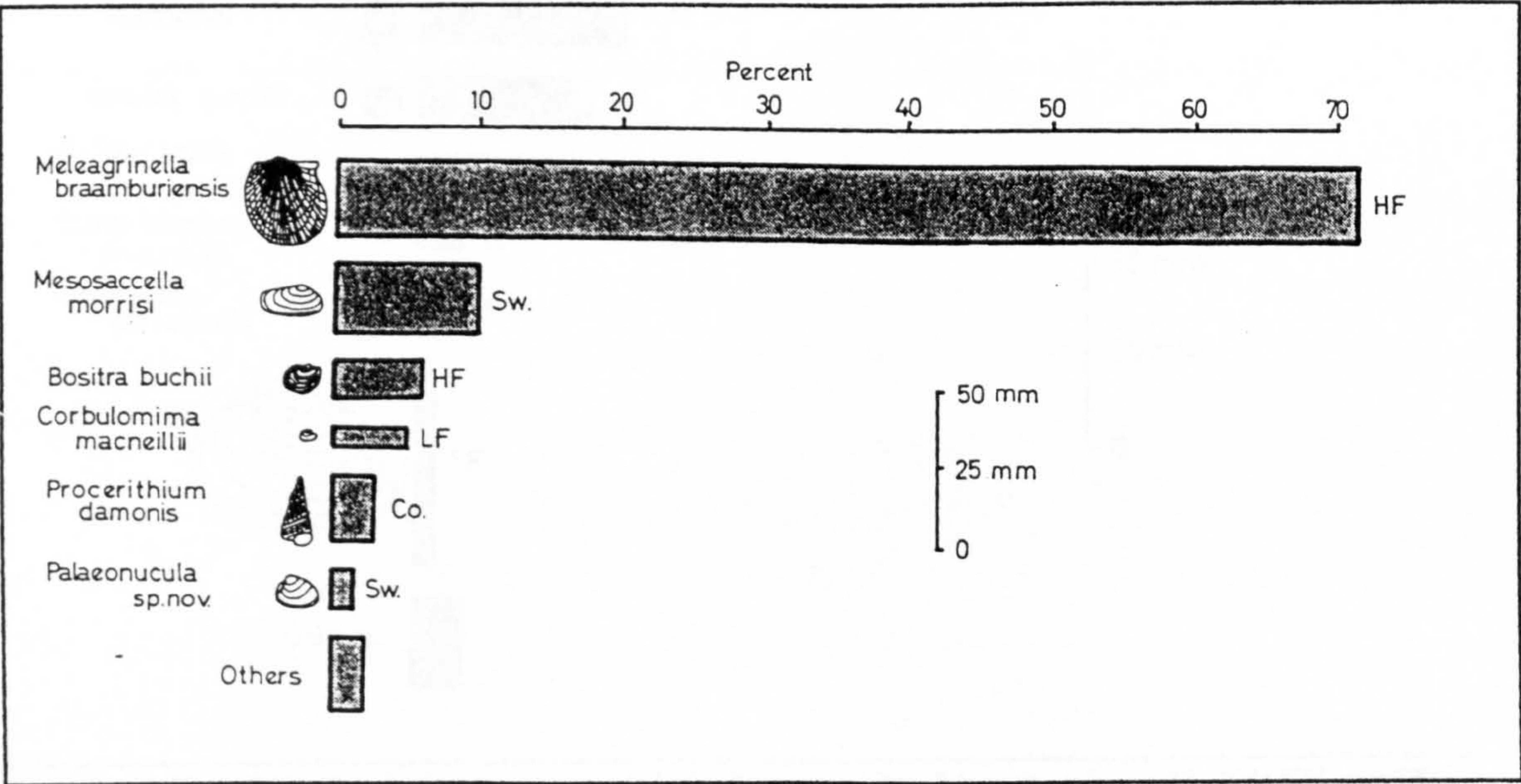


Figure 4.6. Trophic group composition of the *Meleagrinnella* shell bed biofacies, from Duff (1975, p.471).

4.2.3 Calcareous clays

This lithofacies is restricted to the upper *grossouvrei* Subzone where it forms regular alternations with the *Meleagrinnella* shell pavements at Calvert pit, beds JC10E, JC10G, JC10J (Figure 3.4). The facies occurs throughout the whole of the *grossouvrei* Subzone at Saxon pit, beds JS20, JS21, JS22, JS29, JS31, JS32, JS38, JS39, JS40, JS41, JS42 and JS43 (Figure 3.6). The main characteristics of the calcareous

clays is their high dominance diversity with five species each more than 10% of the overall faunal composition and an approximately equal distribution of deposit and suspension feeders (Duff 1975, p.471).

The calcareous clays sampled in this study at Calvert pit and Saxon pit are dominated by *Mesosaccella* with *Meleagrinnella*, showing that both genera coexisted; they are dispersed throughout the lithofacies.

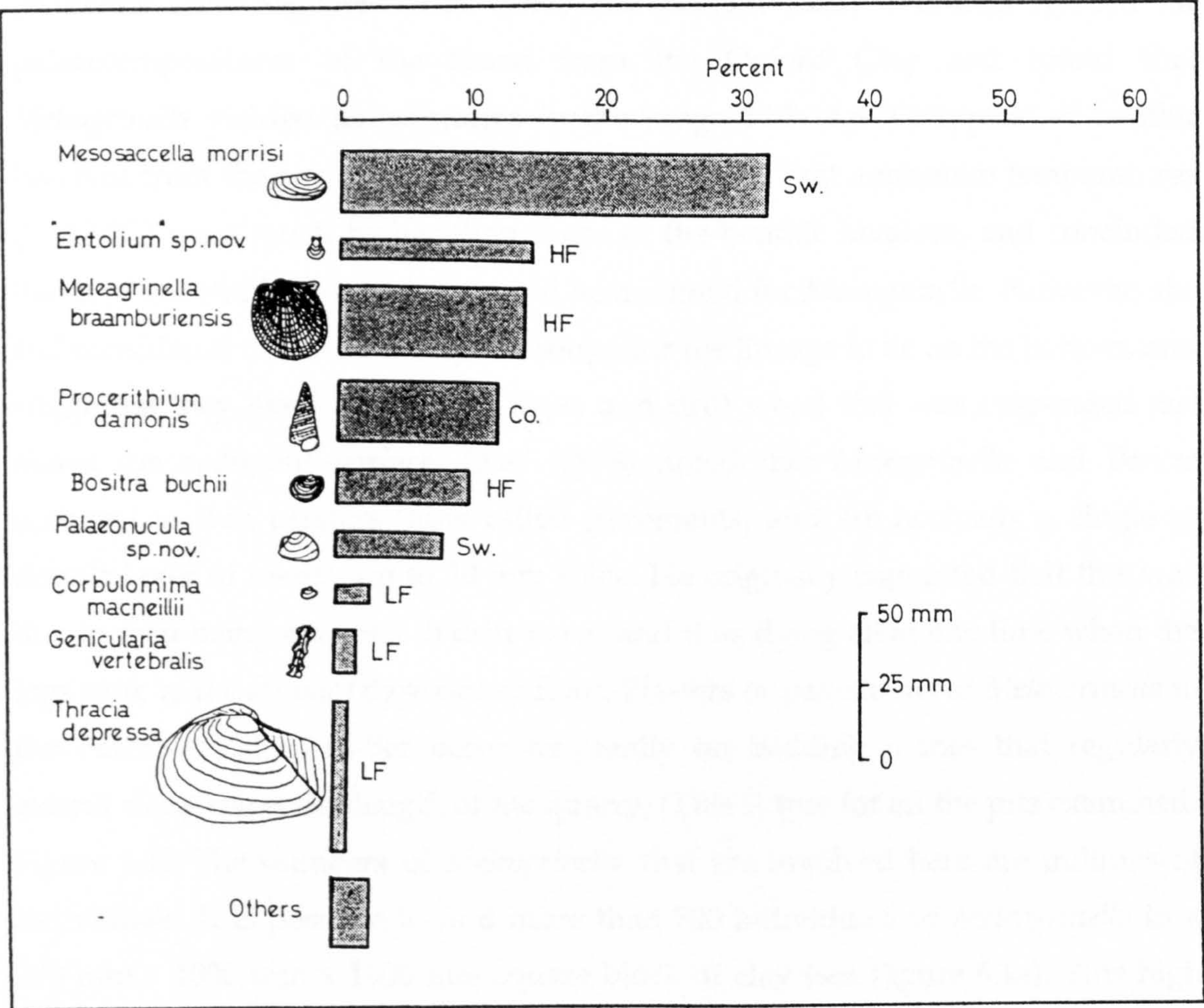


Figure 4.7. Trophic group composition of the calcareous clay biofacies, from Duff (1975, p.473).

4.2.4 Life habit of *Meleagrinnella*

New geochemical data shows that the epifaunal bivalves (*Meleagrinnella* and *Bositra*) could have lived attached to the sea floor. Previously workers have assumed a 'pendent' life habit for *Meleagrinnella* (Duff 1975; 1978). Duff (1978, p.16) claimed that 'in view of the very soft nature of the Oxford Clay substrate, it is unlikely that pectinaceans could have survived lying directly on the sea floor, so a pendent mode of life is postulated.' Duff considered that *Meleagrinnella* would have

attached itself to floating wood and plant debris to survive above the sediment-water interface. Duff (1975) also suggested that the sediment/water interface might have been hostile, thus leading to a reduced diversity of the fauna. Hudson & Martill (1991, p.369) considered the nekton of the Oxford Clay to be diverse, but the benthos not diverse, and suggested this was due to a combination of dysoxic bottom waters and a soft, at times almost fluid, substrate.

A pendent mode of life for *Meleagrinnella* has been questioned previously (Williams 1988; Sageman *et al.* 1991) (see Section 1.2.8). Williams studied the palaeotemperatures of the fauna from the Oxford Clay and found that *Meleagrinnella* yielded temperatures in the range 12.7-14.8 °C, typical of benthic bivalves from the same formation. She also showed that ammonite temperatures (18-23 °C) were much higher than those of the benthic bivalves, and concluded that a near-benthic mode of life could be assumed for *Meleagrinnella*. However, she still considered the Oxford Clay too soupy for the lineage to lie on the bottom, and suggested they lived attached to algae and drift wood that was suspended just above the sediment surface. Duff (1978) noted that *Meleagrinnella* and *Bositra* occurred in thin plasters (now called pavements) and are normally a single or double layer of fossils, up to 20 mm thick. He originally suggested that this was due to their being attached to drift wood and thus dying all at one time when the logs sank to the anoxic/dysoxic sea floor. Plasters or pavements of *Meleagrinnella* in the Peterborough Member occur frequently on bedding planes that regularly extend along the entire length of the quarry. (This is true for all the pits examined, Figure 1.1). The numbers of *Meleagrinnella* that are involved here are millions of individuals. It is possible to find more than 700 individuals of *Meleagrinnella* in a 200 mm x 1000 mm x 1000 mm square block of clay (see Figure 6.1a). This high density can be found over wide areas and almost certainly represents colonisation events (Hudson & Martill 1991). In addition, there is not enough fossilised driftwood to account for the population of bivalves preserved within the beds examined. Furthermore, *Meleagrinnella* has a light, thin and wide shell, suggesting that it was perhaps adapted to exist on softer substrates.

Duff (1975, p.465) also postulated that the pendent bivalves were attached to organic material within the zone of maximum turbidity, allowing use to be made of the superabundant food source. However, the light thin shell of *Meleagrinnella* would almost certainly not have survived within a turbulent

environment. The evidence suggests that *Meleagrinnella* was probably a benthic opportunist which invaded the seafloor when conditions were such that they were able to recline on soft substrates without sinking, and died in mass mortality events during the onset of environmental changes; this explains why there are bedding planes of pavements of *Meleagrinnella*. This suggests the Oxford Clay sea floor was probably periodically 'soupy'.

4.2.5 Facies at Calvert landfill site

Table 4.1 below illustrates changes in biofacies through the Peterborough Member at Calvert pit, according to individual beds as determined by Duff (1975; 1978).

SUBZONE	BED NUMBER	BIOFACIES
<i>phaeinum</i> Subzone	JC12	Foraminifera-rich Bituminous Shale Biofacies
<i>grossouvrei</i> Subzone	JC11	Nuculacean Shell Bed Facies
	JC10K	<i>Meleagrinnella</i> -rich Bituminous Shale
	JC10J	Calcareous Clay Lithofacies
	JC10H	<i>Meleagrinnella</i> -rich Bituminous Shale
	JC10G	Calcareous Clay Lithofacies
	JC10F	<i>Meleagrinnella</i> -rich Bituminous Shale
	JC10E	Calcareous Clay Lithofacies
	JC10D	Foraminifera-rich Bituminous Shale
	JC10C	Deposit-feeder Bituminous Shale Biofacies
	JC10B	<i>Grammatodon</i> Shell Bed Biofacies
	JC10A	Deposit-feeder Bituminous Shale Biofacies
	JC9	<i>Grammatodon</i> -rich Bituminous Shale/ <i>Grammatodon</i> Shell Bed
	JC8	Deposit-feeder Bituminous Shale Biofacies
<i>obductum</i> Subzone	JC7	Nuculacean Shell Bed Biofacies
	JC6	Deposit-feeder Bituminous Shale Biofacies
	JC5	Nuculacean Shell Bed Biofacies
	JC4	Foraminifera-rich Bituminous Shale Biofacies
<i>jason</i> Subzone	JC3C	Foraminifera-rich Bituminous Shale Biofacies

Table 4.1. Biofacies within Calvert landfill site, Buckinghamshire, by beds. (Bed numbers are after Duff (1974)).

Beds JC10F, JC10H & JC10K have previously been described as *Meleagrinnella* shell beds by Duff (1975); however they are now termed *Meleagrinnella*-rich bituminous shale. These beds are not composed of just *Meleagrinnella*, unlike the nukulacean shell beds where the bed is dominantly composed of shells with little mud, e.g. bed JC5, but consists of *Meleagrinnella* shell pavements in a normal bituminous shale with deposit-feeders such as *Mesosaccella* and *Procerithium*.

4.2.6 Facies at Orton brick pit

The sequence at Orton pit is less complete than at Calvert pit or Saxon pit (Table 4.2). The *obductum* Subzone exists at Orton pit but there is little if any of the *grossouvrei* Subzone, due to glacial removal.

SUBZONE	BED NUMBER	BIOFACIES
<i>obductum</i> Subzone	JO15	<i>Grammatodon</i> Shell Bed Biofacies
	JO14	Deposit-feeder Bituminous Shale Biofacies / <i>Meleagrinnella</i> Shell Pavements
<i>jason</i> Subzone	JO13	<i>Gryphaea</i> Shell Bed Biofacies

Table 4.2. Biofacies at Orton brick pit, Peterborough, by beds. Bed numbers are after Duff (1974).

4.2.7 Facies at Saxon brick pit

Saxon pit has one of the largest exposures of the Peterborough Member, from the base of the *obductum* Subzone up through to the Stewartby Member. Table 4.3 illustrates the bed-by-bed changes in biofacies investigated in this study.

SUBZONE	BED NUMBER	BIOFACIES
<i>phaeinum</i> Subzone	JS43	Calcareous Clay Lithofacies
	JS42	Calcareous Clay Lithofacies
	JS41	Calcareous Clay Lithofacies
	JS40	Calcareous Clay Lithofacies
	JS39	Calcareous Clay Lithofacies
	JS38	Calcareous Clay Lithofacies
<i>grossouvrei</i> Subzone	JS37	Nuculacean Shell Bed Biofacies
	JS36	Deposit-feeder Bituminous Shale Biofacies
	JS35	Nuculacean Shell Bed Biofacies
	JS34	Deposit-feeder Bituminous Shale Biofacies
	JS33	<i>Meleagrinnella</i> Shell Pavement Biofacies
	JS32	Calcareous Clay Lithofacies
	JS31	Calcareous Clay Lithofacies
	JS30	<i>Meleagrinnella</i> Shell Pavement Biofacies
	JS29	Calcareous Clay Lithofacies
	JS28	Deposit-feeder Bituminous Shale Biofacies
	JS27	<i>Meleagrinnella</i> Shell Pavement Biofacies
	JS26	Deposit-feeder Bituminous Shale Biofacies
	JS25	Nuculacean Shell Bed Biofacies
	JS24	Deposit-feeder Bituminous Shale Biofacies
	JS23	Nuculacean Shell Bed Biofacies
	JS22	Calcareous Clay Lithofacies
	JS21	Calcareous Clay Lithofacies
	JS20	Calcareous Clay Lithofacies
	JS19	Nuculacean Shell Bed Biofacies
	JS18	Deposit-feeder Bituminous Shale Biofacies
<i>obductum</i> Subzone	JS17	Nuculacean Shell Bed Biofacies
	JS16	Deposit-feeder Bituminous Shale Biofacies
	JS15	Deposit-feeder Bituminous Shale Biofacies
	JS14	Deposit-feeder Bituminous Shale Biofacies / <i>Meleagrinnella</i> Shell Pavement Biofacies

Table 4.3. Biofacies at Saxon brick pit, Peterborough, by beds. Beds numbers are after Hudson & Martill (1994).

4.3 Previous lithofacies and microfacies of the Peterborough Member

Macquaker (1994) initiated a study of the lithofacies present in the Oxford Clay Formation to determine the main sedimentary factors controlling the development of mudstones, and the environmental conditions under which they were deposited. Since then a more detailed study of the lithofacies has been undertaken by Macquaker & Howell (in press) within the *obductum* and beginning of the *grossouvrei* Subzones at Saxon pit (Figure A4.1, Plate A4.1) (see Appendix 4). Previously this part of the succession at King's Dyke pit, Whittlesey has been described as 'the most uniform part of the succession' (Hudson & Martill 1994, p.119). Recently however, this part of the succession has been shown to have many changes in lithofacies (Macquaker & Howell in press).

Combined optical, electron optical and sedimentary logging were used to reveal that the lithofacies included clay-rich mudstones, silt-rich mudstones, shell pavements and shell beds. Most of the mudstones were highly bioturbated; some, however, exhibited remnant upward-fining couplets on a millimetre scale (Plate A4.2).

In the section studied by Macquaker & Howell (in press), five upward-coarsening intervals (metre scale) were observed. These intervals had clay-rich mudstones at their base and coarsened to silt-rich mudstones at their tops. Shell *pavements* were found between the lower two upward-coarsening intervals and in contrast, shell *beds* were found between the upper two upward-coarsening intervals (Plates A4.3-A4.8 and Figure 4 from Macquaker & Howell in press, see Appendix 4 for copy).

The bioturbated millimetre scale upward-fining couplets were interpreted to be individual beds, as a consequence of storm deposition. The presence of bioturbation between storm events obscured most of the internal structures of these units, and was interpreted to indicate a significant amount of time between storms. The metre-scale stacked upward-coarsening successions were interpreted to be parasequences (a relatively conformable succession of genetically related beds or bedsets bounded by marine-flooding surfaces and their correlative surfaces (Van Wagoner 1985)). The level between parasequences where there is rapid sediment fining were interpreted to be flooding surfaces/parasequence

boundaries.

Macquaker & Howell (in press) also discussed the variability within samples collected from the same unit (3 m below the top of bed JS14) in Saxon and King's Dyke pits. (The distance between these two pits is approximately 1 km). Plates A4.9-A4.11 illustrate that there is no systematic facies or grain-size variability within an individual pit (see Plates A4.9, A4.10 and A4.11 A-F), yet comparison of samples from the two pits suggests that those from King's Dyke (Plate A4.11 G-L) are slightly coarser. Thus they concluded that those samples from closely spaced locations (< 0.05 km) have similar silt:clay ratios and are the same lithofacies, whereas samples from more widely spaced locations (0.06 to 3.0 km) have widely varying silt:clay ratios and are not the same lithofacies.

Evidence from the study undertaken by Macquaker & Howell (in press) suggests that there are changing facies within this 'homogenous' mudstone succession on a bed, parasequence and parasequence set scale, as well as on a lateral 0.1-1.0 km scale (Plates A4.3-A4.11 and Figure 4 from Macquaker & Howell in press, see Appendix 4 for copy). These results are utilised within Chapter 6 (Section 6.3.2), where evidence for changing environmental conditions is discussed.

4.4 Evidence of depositional environment from differing facies

During the deposition of the bituminous shales facies Duff (1975) suggested that a gradual recession of the shore line during deposition of the transition beds into the Oxford Clay Formation eventually allowed the establishment of quiet water conditions in which the bituminous shales were deposited. At Peterborough and Calvert this phase seemed to have begun more or less at the start of the *jason* Subzone. There followed thick, dominantly deposit-feeder bituminous shales, which occupied the whole of the *jason* and *obductum* Subzones at Peterborough and Calvert, with the exception of the 1 m band of blocky claystone at Calvert (Duff 1975, p.474). During this time the bottom conditions were quiet and water circulation was probably poor, producing impoverished faunas of benthonic suspension-feeders. Duff (1975, p.474) thought these lived above the bottom and attached to postulated organic material - pendent epifaunal suspension feeder bivalves - chiefly *Bositra buchii*, *Meleagrinella braamburiensis* and *Oxytoma*

inequivalve. However, as previously mentioned (Section 4.2.4) this 'pendent' mode of life is now considered incorrect.

Throughout the East Midlands, the end of the *obductum* Subzone coincides with a widespread phase of slow deposition, marked by nuculacean shell beds (Bed JC5 at Calvert Landfill Site and bed JS17 at Saxon Brickpit, Figures 3.4 & 3.6). By the start of the *Groussouvrei* Subzone subsidence occurred and oxygenation of the water gradually decreased, with the deposit-feeder bituminous shales being replaced by numerous different facies (Tables 4.1 & 4.3), the deposit-feeder rich bituminous shales never became re-established (Duff 1975, p.475). There was a renewed phase of shallowing, which produced the characteristic alternation of calcareous clays and *Meleagrinella* shell pavements later in *grossouvrei* Subzone times, bringing the Middle Callovian to a close in southern England (Duff 1975, p.475). This sequence of *Meleagrinella* shell pavements probably produced small non-sequences (hiatuses). Aeration in the calcareous clays must have been relatively good as they supported a diverse fauna of epifaunal and infaunal bivalves. The *grossouvrei* Subzone concluded over the whole area by a thick nuculacean shell bed, the Comptoni Bed, (bed JC11 at Calvert pit and bed JS37 at Saxon pit, Figures 3.4 & 3.6). This is usually capped by the Acutistriatum Bed, the basal bed of the *phaeinum* Subzone (bed JC12 at Calvert pit, and bed JS38 at Saxon pit, Figures 3.4 & 3.6).

4.5 Biofacies model for the Peterborough Member

Duff (1975) described the Peterborough Member as a bituminous shale which he thought formed during periods of relative sea level rise and highstand. Most organic-rich sequences have been interpreted as being representative of long-term stagnation with anoxic conditions predominant in all but the uppermost wave-mixed layers of the water column - the stagnant basin model (Sageman *et al.* 1991). However, this may be inappropriate for the Oxford Clay Formation, which was more likely to be deposited within an oxygen-deficient shallow marine basin (see Sections 1.2.8 and 1.2.9). Numerous authors have discussed this environment (e.g. Rhoads & Morse 1971, Savrda *et al.* 1984, Thompson *et al.* 1985, Kammer *et al.* 1986, Savrda & Bottjer 1987, Wignall & Myers 1988 and Oschmann 1993). An oxygen-

deficient facies normally comprises dark-coloured, organic carbon and pyrite-enriched rocks which range from extremely well-laminated oil shales and bituminous shales to various types of marls and limestones (some of which occur within the Oxford Clay Formation). Rhoads & Morse (1971) described the original biofacies model (Figure 4.8) in which they characterised three distinct biofacies: anaerobic, with laminated sediments and no macrofauna (oxygen <0.1 ml/l, or effectively anoxic); dysaerobic, with slightly burrowed sediments and a sparse soft-bodied infauna (oxygen 0.1 to 1.0 ml/l, or dysoxic); and aerobic, with bioturbated sediments and abundant and diverse faunas (oxygen >1.0 ml/l, or oxic). Figure 4.8 includes the revised model of Rhoads & Morse (1971) by Savdra *et al.* (1984), Thompson *et al.* (1985) and Savdra & Bottjer (1987).

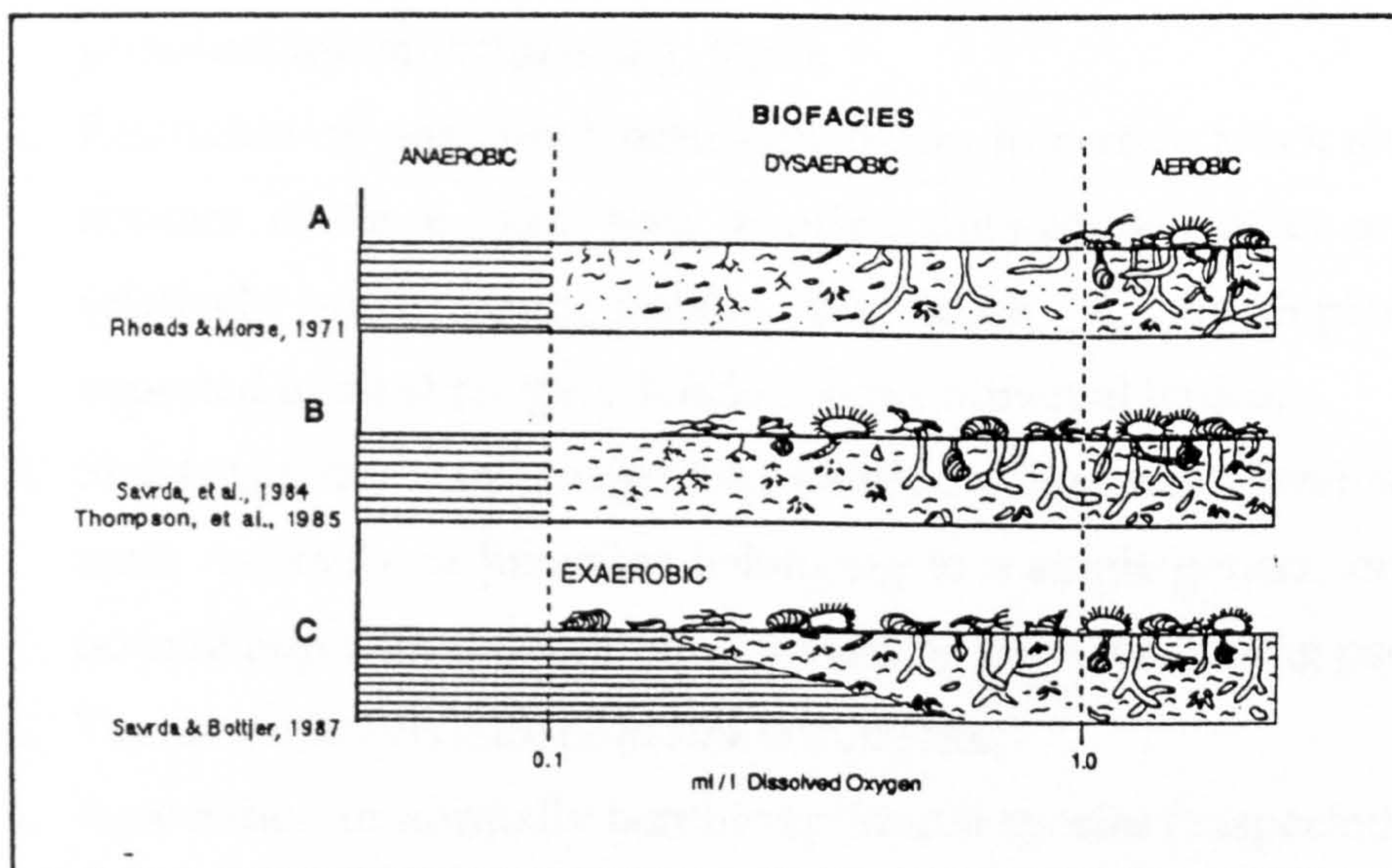


Figure 4.8. The Rhoads & Morse (1971) biofacies model for oxygen-deficient environments. Revision of the Rhoads & Morse (1971) model includes: B, the models of Savdra *et al.* (1984) and Thompson *et al.* (1985) in which new dysaerobic faunas are recognised; and C, the model of Savdra & Bottjer (1987), in which a new subunit of dysaerobic biofacies the 'exaerobic zone' is proposed, from Sageman *et al.* (1991, p.543).

The Peterborough Member (which is highly bioturbated with a diverse fauna through most of its sediments) falls broadly into the aerobic biofacies of the models in Figure 4.8. Most revisions of the original Rhoads & Morse (1971) model (Savdra *et al.* 1984, Thomspson *et al.* 1985, Savdra & Bottjer 1987, Wignall & Myers

1988, Oschmann 1993) have focused on the character and biota of dysaerobic biofacies. However, Sageman *et al.* (1991, p.544) have shown that abundant shelly and soft bodied infauna and epifauna can survive at oxygen levels as low as 0.3 ml/l, significantly altering the biotic and sedimentological character described by Rhoads & Morse (1971), suggesting the Oxford Clay could have been less than aerobic. Sageman *et al.* therefore suggested the need for further revisions of accepted models, due to the occurrence of numerous extremely well-laminated black shales containing fossil assemblages of *in situ* epifaunal organisms. Previously, it has often been assumed that these fossils could be interpreted as pseudoplanktonic (Duff 1975), therefore leaving the sediment/water interface within the anaerobic zone; however, Sageman *et al.* (1991, p.544) argue against a pseudoplanktonic mode of life due to:

1. The great abundance of fossils compared with relative scarcity of suspected pseudoplanktonic floats (e.g. logs);
2. Restriction of supposed pseudoplankton to certain black shale intervals, and absence of these same taxa in other time-equivalent or successive facies; a relatively even stratigraphic distribution of pseudoplankton would be expected in most oxygen-deficient epicontinental basins;
3. Size-frequency data suggesting benthic colonisation events and subsequent mass mortality of juveniles belonging to a single generation whereas a more normal population distribution would be expected among pseudoplankton;
4. Taphonomic evidence of *in situ* occurrence;
5. Association of normally benthic epifaunal species (suspected pseudoplankton) with free-living epifaunal and infaunal taxa which are functionally incapable of attachment to floating sites;
6. Alternation of beds containing predominantly infauna or predominantly epifauna, suggesting ecologic exclusion among benthic taxa (trophic amensalism: Rhoads & Young 1970); and
7. Relatively rare pseudoplanktonic encrustation of potential hosts in modern and ancient marine environments (including floating logs, seaweed, cephalopods, etc.).

Sageman *et al.* (1991, pp.549-551) developed a new biofacies model by studying the faunal assemblages which represented different types of environments. Under their classification scheme there were 2 types of fossil assemblage: 'fossil assemblage of type 1 palaeoenvironments'; and 'fossil assemblages of type 2 palaeoenvironments' (Figure 4.9). Type 1 was an environment with a sharp boundary, at or near the sediment-water interface, between anoxic sediments and a dysoxic to oxic water column. Fauna within this palaeoenvironment included calcareous benthic foraminifera, numerous trace fossils (including *Planolites*, *Chondrites*, *Teichichnus*, *Trichichnis*, *Thalassinoides* and *Rhizocorallium*), and body fossils; which typically included infaunal filter-feeding and detritus-feeding bivalves, linguloid brachiopods, aphorraid gastropods, epibenthic ammonites, and other molluscs (Duff 1975). Diversity within this palaeoenvironment was moderate to high in most cases and deposit feeding was considered the dominant trophic strategy (Sageman *et al.* 1991).

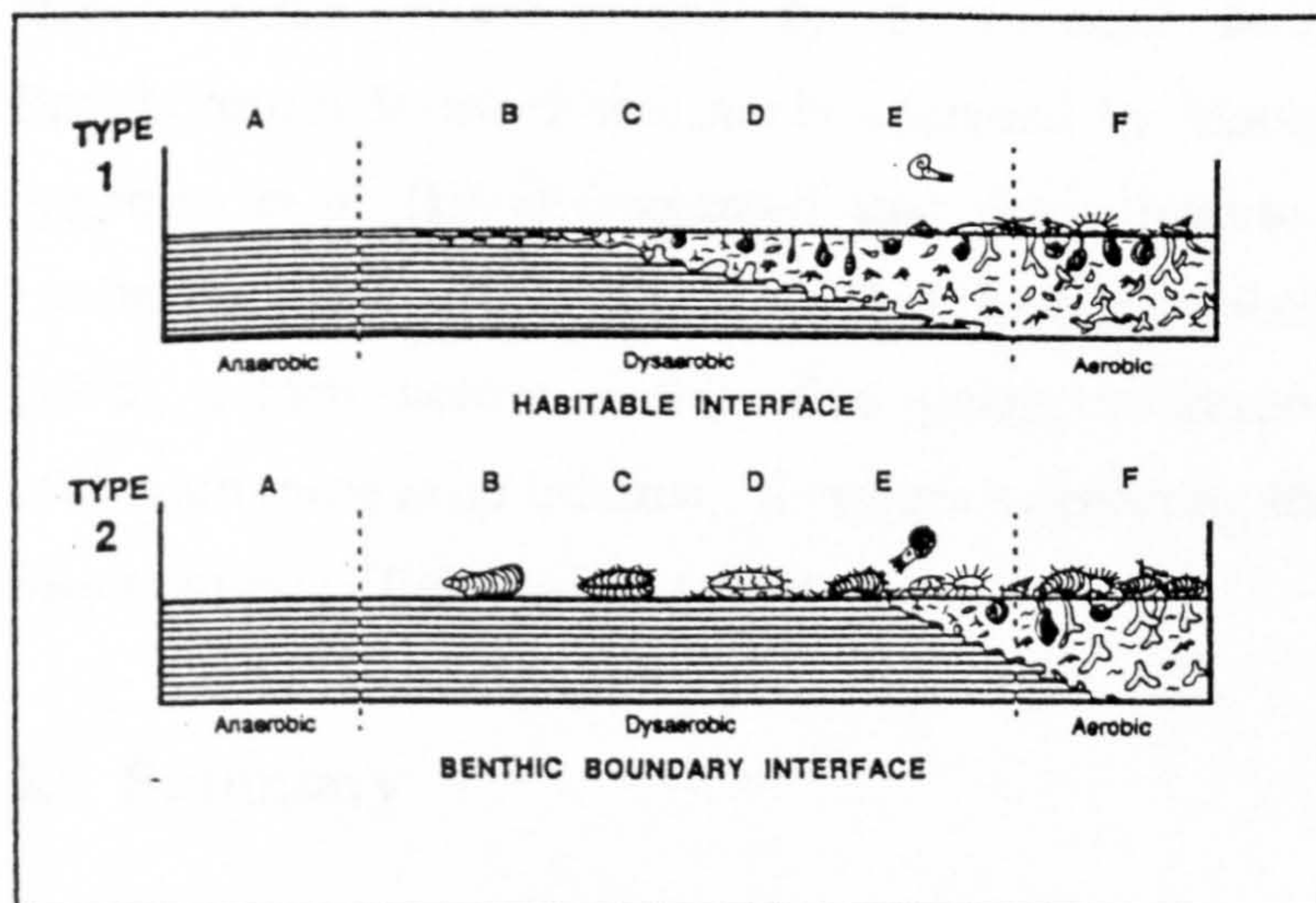


Figure 4.9. A comprehensive biofacies model for black shales with Type 1 and Type 2 redox gradients. Letters A-F represent biofacies levels that correspond to a specific level of bottom water oxygenation and a specific substrate type: habitable substrates in Type 1 biofacies and benthic boundary substrates in Type 2 biofacies. From Sageman *et al.* (1991, p.557).

The Type 2 assemblage is typically dominated by small, thin-shelled epifaunal bivalves or brachiopods. The bivalves represent groups of 'flat clams' that may have evolved special adaptations for survival in low-oxygen environments, e.g. thin, broad shells for habitation on soft substrates, and

expanded gill and mantle tissues for greater oxygen absorption. They typically occur as discrete event communities, suggesting brief opportunistic colonisation events in response to changes in bottom water oxygen or the nature of the substrate (Sageman *et al.* 1991).

The Peterborough Member consists mainly of the bituminous facies (Tables 4.1, 4.2 and 4.3) which falls well into 'fossil assemblage of type 1 palaeoenvironments' as described above, the dominant trophic strategy being deposit-feeding with a moderate to high diversity of fauna. The *Meleagrinnella* shell pavements which dominate the *obductum* and parts of the upper *grossouvrei* Subzones within the Peterborough Member (Tables 4.1, 4.2 and 4.3) are considered to be part of 'fossil assemblage of type 2 palaeoenvironments' as described above. The thin, broad shell of *Meleagrinnella* has adapted in response to softer substrates (Section 4.2.4), and occurs in pavements on bedding planes, illustrating brief opportunistic colonisation events in response to the changing substrate.

Sageman *et al.* (1991) suggested that the substrate is habitable in type 1 environments, characterised by bioturbated sediments. (This is true for Peterborough Member sediments analysed by Macquaker & Howell (in press)). Sageman *et al.* (1991) suggested that the substrate is uninhabitable in type 2 environments, however we found that the *Meleagrinnella* shell bed biofacies of Duff (1975), which occurs within this palaeoenvironment, is highly bioturbated (although there is no infauna), therefore suggesting that even these new models of Sageman *et al.* (1991) require review.

4.6 Summary

Within this relatively thin sequence of the Peterborough Member (12-18 m), occupying just over four ammonite Subzones, there are two cycles of environmental changes recorded by Duff (1975). Firstly, there is the deepening sequence from the Kellaways Formation through the transition beds into the deposit-feeder bituminous shales of the *jason-obductum* Subzones. Secondly, there is a cycle within the *grossouvrei* Subzone: distinct deepening and shallowing phases, ending with a pronounced non-sequence.

Duff (1975; 1978), Hudson (1978), Martill & Hudson (1991) and Hudson & Martill (1994) have proposed that the Oxford Clay mudstones of central England

were deposited in a relatively shallow, productive, epeiric sea. The absence of macro-sedimentary structure suggested that these mudstones were intensely bioturbated and the bottom waters were oxygenated. However, Duff (1978, p.16) suggested that conditions at the sediment-water interface were fairly hostile, either dysoxic or the sediment was 'soupy' (Martill *et al.* 1994) which led at times to reduced diversity of the benthic fauna.

Previously (Hudson 1978 and Fisher & Hudson 1987), it has been suggested that pyrite present within the formation at times showed that the pore water in these muds quickly became reducing and 'anoxic/sulphidic', once the sediment had been buried. Recently however, Macquaker & Howell (in press) suggested that the bioturbated millimetre scale upward-fining couplets, produced by storm deposition, showed subsequent bioturbation between the storm events (illustrated by the presence of *Planolites isp.* within the couplets), suggesting that soon after deposition the pore waters were sub-oxic. Taken together with the absence of laminae in all samples, and an oxic ichnofacies assemblage, this indicates that the pore waters within a few mm of the surface were neither anoxic nor fully oxic.

The thinness of the ammonite zones and presence of shell beds and shell pavements within the Peterborough Member suggested that sedimentation was not continuous, containing many hiatuses. Hudson & Martill (1991) suggested that deposition was extremely episodic, with relatively long periods of either erosion or non-deposition being interrupted by relatively short periods of rapid sediment accumulation. Macquaker & Howell (in press) recognised that storms were probably responsible for the sedimentation, and that they produced beds that were only millimetres thick. This observation and the fact that the individual beds were colonised strongly suggested that there were significant hiatuses between storm events. They suggested, in light of these observations, that the millimetre-scale hiatuses represented substantial amounts of time, and that hiatuses were not only occurring at the shell-beds and concretionary horizons but all the way through the Peterborough Member. Although the preserved sedimentary record can only ever represent a fraction of the geological history, the stratigraphical completeness is considered to be fairly high within the section of Peterborough Member studied by Macquaker & Howell (in press) (*obductum* to base *grossouvrei* Subzones). Every time a storm occurs, within this section of the Peterborough Member, some sediment is deposited, even if the storms were only

every 100 years there would be stratigraphical completeness at the 100 year level. It is probably that little erosion would have taken place after deposition of the storm beds, only significant hiatuses. Thus the Peterborough Member is considered an excellent place to study microevolutionary patterns as the stratigraphical completeness at the level of storm deposition would have been extremely high, if not 100% complete.

CHAPTER 5

LABORATORY & STATISTICAL METHODS

5.1 Preparation techniques

Samples were removed from the sections chosen in each of the pits as described in Section 3.3. On returning to the laboratory, the specimens were removed from the polythene bags and tissue wrap, sprayed with PVA glue to ensure preservation, and then placed on a bench for at least 24 hours to ensure the glue spray completely penetrated the clay and dried. The specimens were then boxed and labelled. Before measuring the specimens it was vital to make sure the whole fossil could be seen, and so dental tools were used to dig tiny amounts of clay away from the edges of each fossil. Once this had been done the fossil could be measured under the microscope. It was not necessary to remove the individual fossils from the clay matrix. The clay moulds of the fauna were left as found, there was no need to take a resin cast, as the mould could be directly measured under the microscope.

5.2 Measuring techniques

Measurements were made using a Nikon binocular microscope (Type 102, magnification from x0.8 - 3.5) and graticule eye piece (100 graduations). Duff, (1978) measured specimens using a pair of vernier callipers. This is highly accurate for specimens free from the matrix; however, the microscope and graticule was determined to be a more accurate way to measure embedded fossils (accuracy was to within 0.1 mm).

The measurements that were taken on the bivalves had to be of use in demonstrating shape/morphological changes. Duff (1978) took measurements on numerous species of bivalve, including the six species chosen for this study (Section 1.1.1, Figure 1.3). The measurements Duff took on the two main species

used in this study were: Length, Height, Anterior Length, Length of the Straight Hinge and Inflation for *M. braamburiensis*; and Length, Height, Anterior Length and Inflation for *M. morrisi*. Inflation was not measured within this study due to difficulties in obtaining specimens which were not deformed. Duff (pers. comm. 1995) thought that this measurement was of limited utility in detecting evolutionary patterns, and that the measurement was very difficult to record accurately.

The same parameters which were measured by Duff (1978) on both *M. braamburiensis* and *M. morrisi*, except inflation, were measured for this study; the Hinge Length on *M. morrisi* and the Density of Ribs on *M. braamburiensis* were also determined. The dimensions outlined above were determined using the following protocols (the parameters are capitalised here for easy recognition):

Length (L) was measured parallel to the long axis of the ligament in most cases (Figure 5.1).

Height (H) was always measured as the maximum dimension perpendicular to the length, passing through the umbones and the ventral margin (Figure 5.1).

Anterior Length (AL) was measured as the distance from the points of the umbones to the anterior margin of the shell, measured parallel to length (Figure 5.1).

Hinge Length (HL) was measured along the length of the straight hinge-line only (Figure 5.1).

Density of Ribs (DR) was determined by measuring a certain distance at right angles from the umbo, parallel to Height (for example 10 mm) and then measuring perpendicular to it at a width of the same measure (i.e. 10 mm). Within this width the number of ribs was then counted (Figure 5.2). On the larger specimens measurements were taken at 5 mm, 10 mm, 15 mm and 20 mm. On complete specimens the DR was also measured for the complete shell.

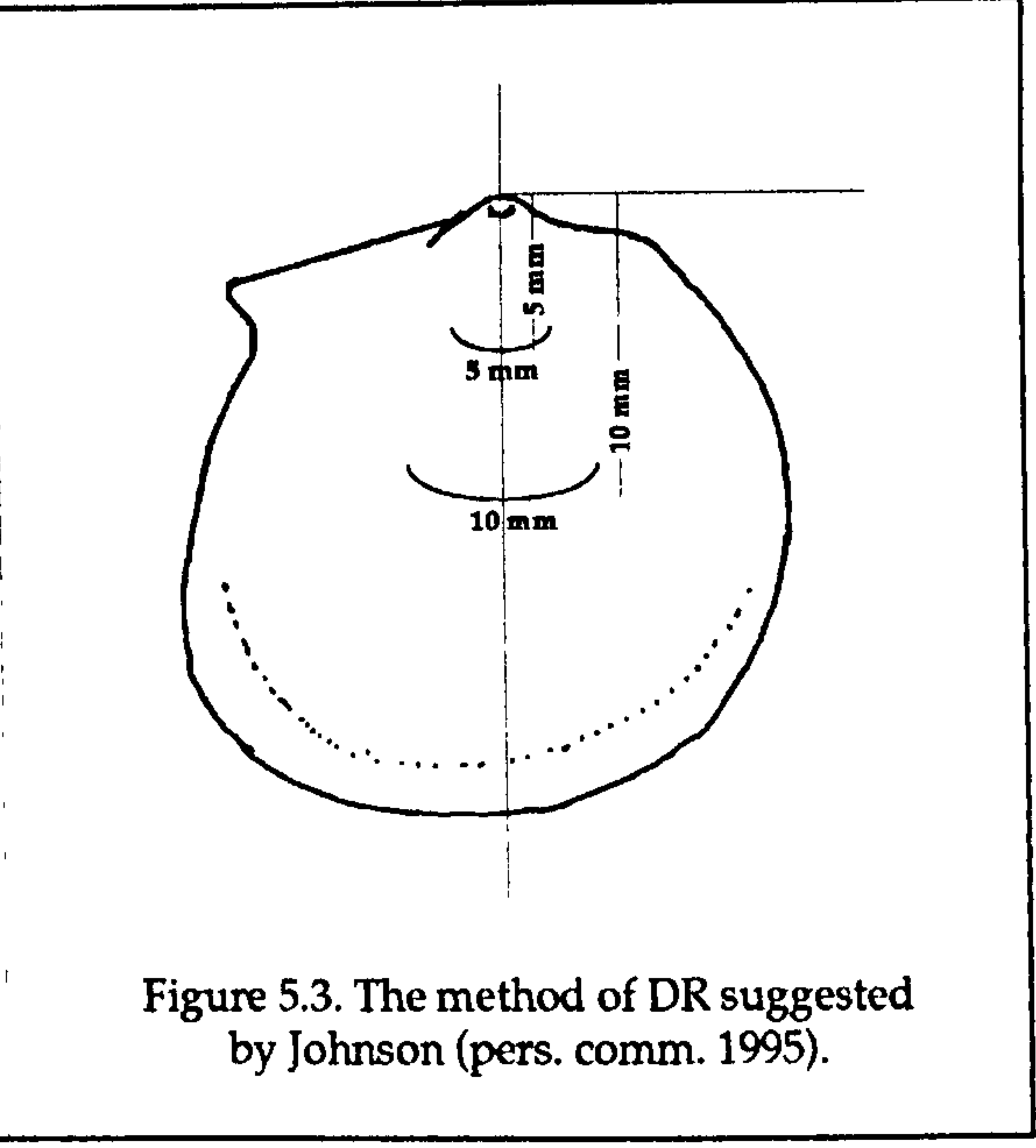
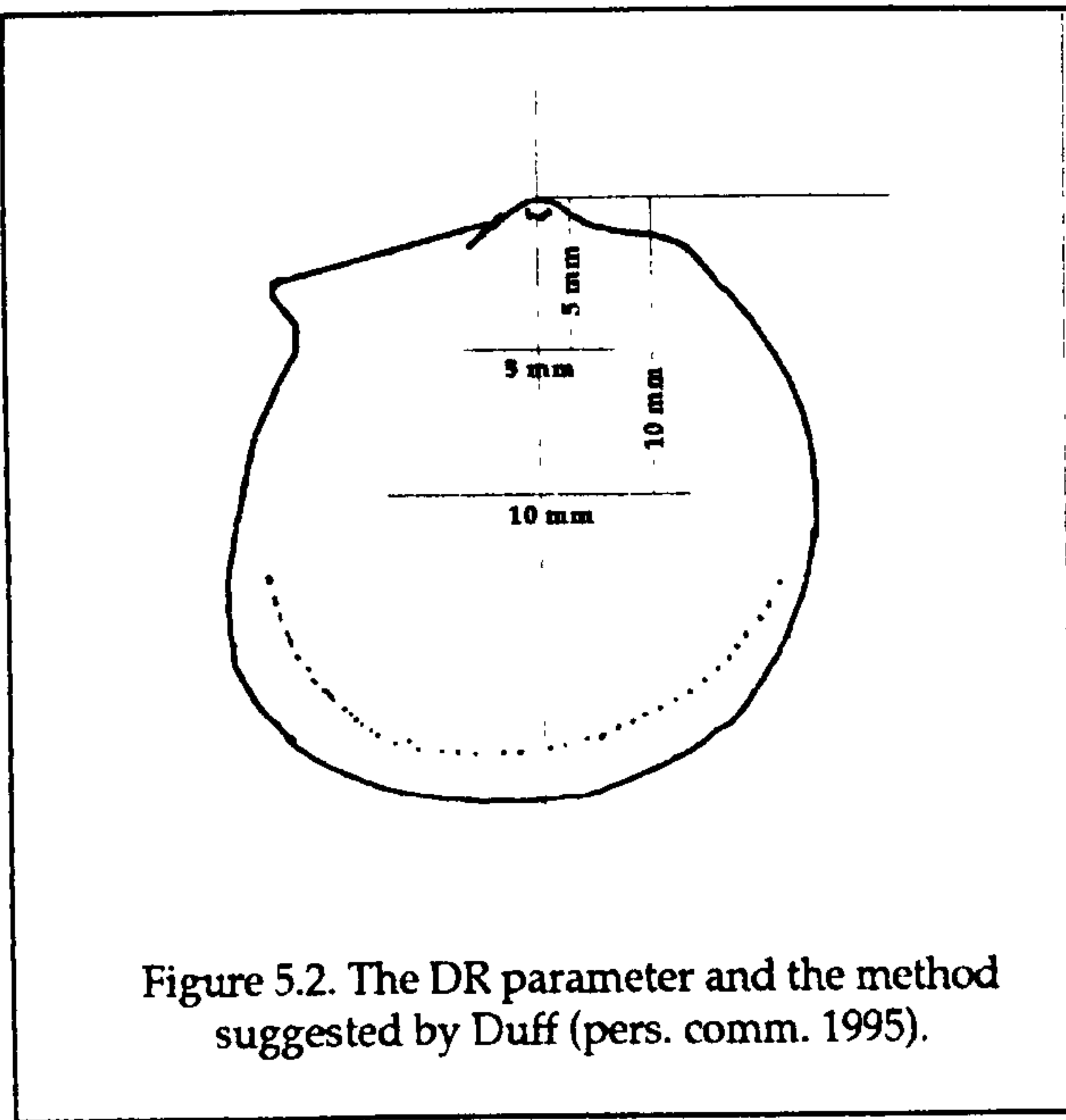
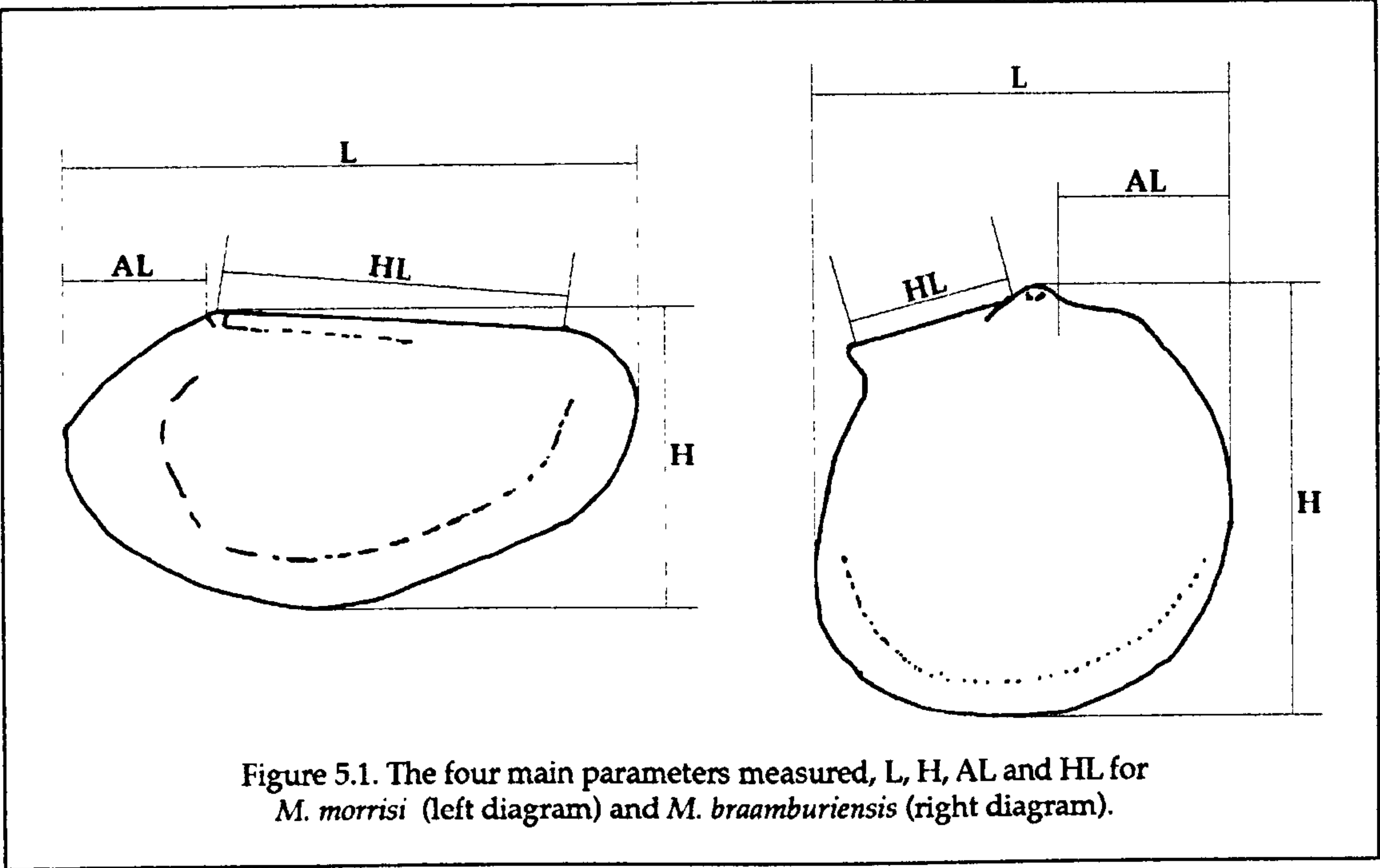
5.2.1 Problems with measuring

Length, Height, Anterior Length and Hinge Length were relatively easy to measure. However, the measurement of the Density of Ribs was problematic. Advice and guidance was obtained from both my supervisors (Dave Martill and Peter Sheldon) and Keith Duff and Andy Johnson. Duff (pers. comm. 1995)

suggested that the best way to obtain an accurate measurement was to measure a certain distance at right angles from the umbo (for example 10 mm) and then measure perpendicular to it. At this distance the primary ribs can be measured. However, the secondary and tertiary ribs do not start to appear until further down the shell. Thus Duff's idea was to measure at greater distances away from the shell as well, and he suggested measuring at 20 mm and 30 mm on the larger specimens. However at these greater distances a width of 10 mm perpendicular to the measure from the umbo was no longer sufficient because the ribbing in these areas is more widely spaced as the shell is larger. Thus at 20 mm from the umbo Duff suggested a measurement of 20 mm should be taken (Figure 5.2). This he thought would allow the variation in shell detail to be observed throughout the specimen as secondary and tertiary ribs became exposed. Duff suggested that measuring along the growth lines to the margins of the shell may be inaccurate because the shell grew quickly along the ventral margin away from the hinge and slower down the sides. Thus a squeezing up of the ornamentation occurs at the edges (because the shell gets larger in the middle), so a measure at the edges gives a false number of ribs as these are compressed.

Andy Johnson suggested a slightly different approach. He suggested taking a measure from the umbo and counting the ribs along a growth line, at that distance away. Johnson (pers. comm. 1995) stated that all points on a growth line were secreted at the same time. Johnson (pers. comm. 1995) suggested that ribs should be counted at several standard distances (e.g. 10 mm, 20 mm, etc.) determined by measuring from the umbo along the lines of maximum growth. This he suggested was worthwhile if the ribs are intercalated or bifurcated during growth (Figure 5.3).

The technique adopted in this study was the 'Duff' method because it was determined that this technique could be adopted repetitively to a higher standard of accuracy than the 'Johnson' technique.



5.2.2 Summary of measuring techniques

The L, H, AL & HL parameters were relatively simple to measure. The DR parameter, however, was a little more complicated, and overall it is considered that this measurement was less accurate than the other parameters measured throughout all three pits.

The L, H, AL & HL are used to illustrate how the shape/morphology of *M. braamburiensis* and *M. morrisi* changed during the section of Peterborough Member from all three pits (Figures 3.4, 3.5 & 3.6, see separate book of figures) (Chapter 7). The DR parameter was also graphed (Section 7.9).

5.3 Statistical methods

Ratios of Length to Height and Hinge Length to Anterior Length, as well as 95% confidence intervals for the ratios were calculated. Means of Length to Height and Hinge Length to Anterior Length ratios were calculated for each 200 mm interval (defined within this study as horizons). The means are graphed against stratigraphy, with their respective error bars (95 % confidence intervals) to show morphological patterns (see Chapter 7). Logarithms for each measurement were also calculated to allow tests to be performed for allometric growth. Further details of the analyses performed for the purpose of testing for allometric growth are given within Section 7.1. In accordance with the suggestions of Erwin & Anstey (1995) (Section 2.4), no other statistical analyses were performed on the actual measurements other than to create ratios as described above.

CHAPTER SIX

ENVIRONMENTAL CHANGE

6.1 Detecting environmental change

This study of microevolutionary patterns within the Peterborough Member includes the detection of patterns from differing environmental conditions.

Environmental conditions in the Peterborough Member are inferred from analyses of the fauna (Section 6.2), lithology (Section 6.3), and a variety of geochemical parameters (Section 6.4), e.g. TOC (total organic carbon).

A considerable thickness of sediment of the same lithology, and with the same faunal composition and geochemical signals, can be considered the product of a relatively stable environment. By contrast, parts of the sequence with numerous thin beds of distinct lithology, changing faunal composition and geochemical signals (through time) are taken to indicate changes in the environmental conditions and thus a more fluctuating environment.

6.2 Palaeontological evidence for environmental change

6.2.1 Bivalve ecology

The mode of life of *Meleagrinnella braamburiensis* was previously discussed in Section 4.2.4. Here it was proposed that *M. braamburiensis* was a benthic opportunist that colonised the sea floor when the sea floor was soft or even 'soupy' in condition. During these times *M. braamburiensis* would have dominated due to its light-weight, thin, wide shell. Shallow infaunal bivalves (mainly *Mesosaccella morrisoni*) would not have survived as they would not have been able to burrow through the 'soupy' layer into the firmer sediment below; this soupy layer was often as much as 200 mm thick (Martill pers. comm. 1997). The pallial sinus of *M. morrisoni* is small, suggesting that its siphons would not have been long enough to reach through the 'soupy' layer.

M. braamburiensis and *M. morrisi* both occur in large numbers, but are almost mutually exclusive (see Figure 6.1a and b); *M. braamburiensis* would have lived during times when the conditions of the sea floor were somewhat 'soupy', whereas *M. morrisi* could occur only in great numbers when the substrate was firmer, allowing it to burrow.

6.2.2 Population study of *M. braamburiensis* and *M. morrisi*

A population study of the bivalves *M. braamburiensis* and *M. morrisi* was undertaken on a horizon basis, i.e. every 200 mm vertically from the *obductum* Subzone to the *phaeinum* Subzone. All the bivalve fauna from the 200 mm x 1000 mm x 1000 mm block of clay was collected and counted. Horizon numbers used within this section can be found graphed against stratigraphy and bed numbers on Figures 3.4-3.6 (see separate book of figures).

The population study for Calvert pit (Figure 6.1a) shows a tendency for little overlap between *M. morrisi* and *M. braamburiensis* in large numbers of individuals. Between horizons 9-25 *M. braamburiensis* is the more dominant bivalve with larger populations than *M. morrisi* (less than 50 at each horizon). There is a sudden peak of *M. braamburiensis* at horizon 22 with more than 700 individuals. The lineage then decreases away to less than 50 by horizon 27. *M. morrisi* from horizon 25 onwards increases quite dramatically in numbers until horizon 38, where *M. morrisi* suddenly declines and a burst of *M. braamburiensis* appears again. The two lineages are virtually mutually exclusive, with only minor numbers of each species present where the other species is represented by large numbers.

The populations for Saxon pit appear to be very similar to that of Calvert pit (Figure 6.1b). As in Calvert pit, *M. braamburiensis* also dominates at the base of the section, with numbers close to 400 in any single horizon. At horizon 16, *M. braamburiensis* has the last of its high populations (115 individuals per 200 mm x 1000 mm x 1000 mm square), *M. morrisi* takes over with 78 individuals. Before this there were less than 15 individuals of *M. morrisi* per horizon. Between horizons 16 and 28 *M. morrisi* dominates with only a few *M. braamburiensis*; above horizon 28, *M. braamburiensis* increases in number once more to a maximum of 300 at horizon 33, with the last large population size at horizon 36 (151 individuals). *M. morrisi* is present during

this second large burst of *M. braamburiensis*, but only once do the numbers of *M. morrisi* exceed 50 (horizon 35, with 57 individuals). Above horizon 37, *M. morrisi* immediately increases in number (horizon 38 has 80 individuals) while *M. braamburiensis* decreases rapidly and dies out completely by horizon 39. Subsequently *M. morrisi* continues to dominate to the top of the section.

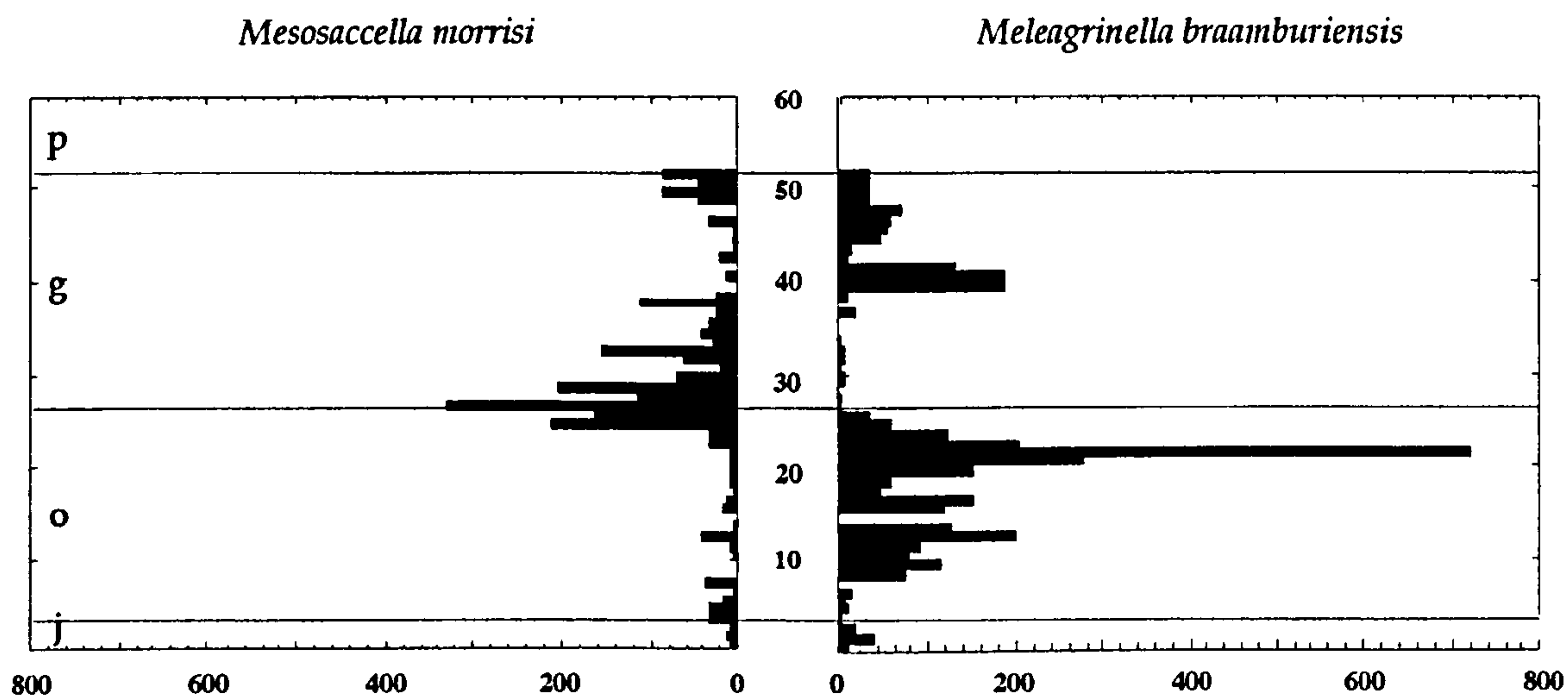


Figure 6.1a. Calvert pit

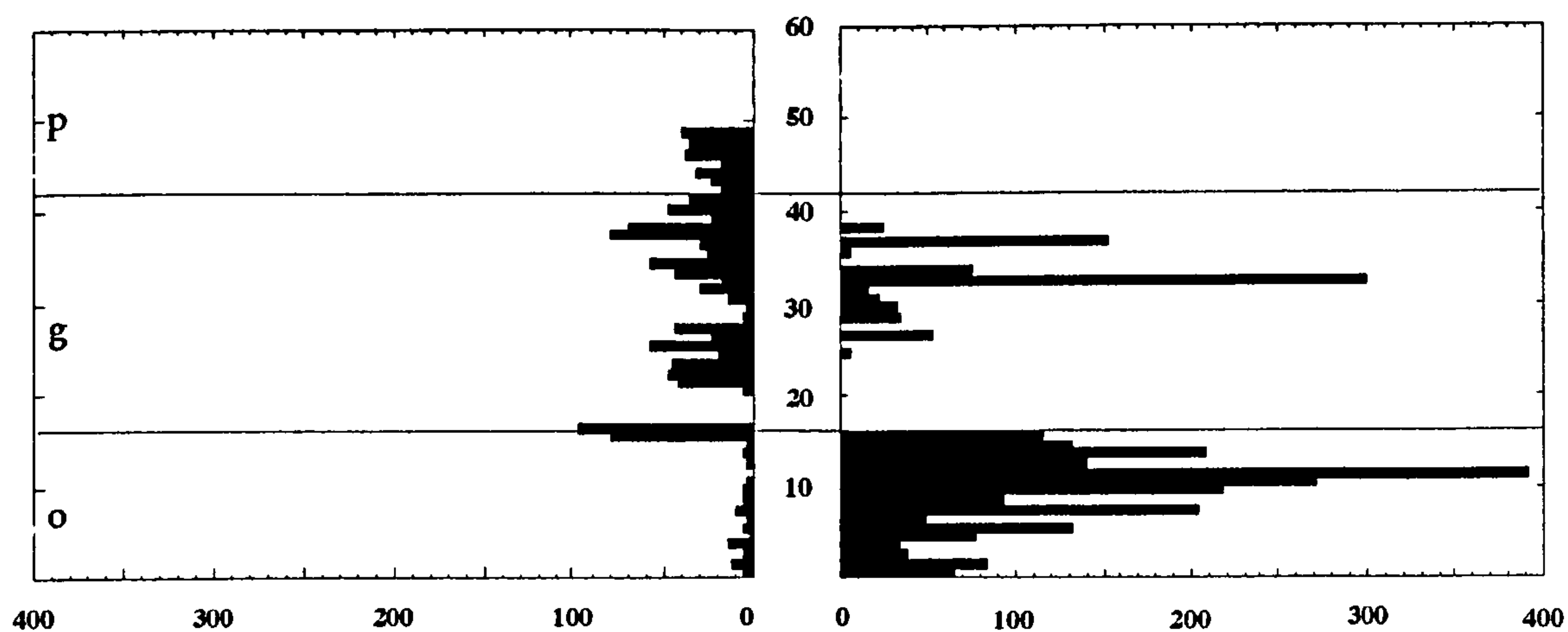


Figure 6.1b. Saxon pit

Figure 6.1a & b. Population data (numbers of individuals per 200 mm x 1000 mm x 1000 mm square block of clay), against horizon number for *M. morrisi* and *M. braamburiensis* at Calvert pit, Buckinghamshire and Saxon pit, Peterborough (j = *jason* Subzone, o = *obductum* Subzone, g = *grossouvrei* Subzone, and p = *phaeinum* Subzone).

M. braamburiensis attained its largest numbers during the *obductum* Subzone, suggesting the Oxford Clay sea floor was more 'soupy' during this time, allowing the soft-substrate adapted *M. braamburiensis* (Section 4.2.4) to attain its large numbers as the infauna (*M. morrisi* etc.) could not burrow through the soupy layer (Section 6.2.1). These epifaunal bivalves were opportunists, colonising the whole of the platform during these times. Later, in the Peterborough Member (*grossouvrei* and *phaeinum* Subzones), *M. morrisi* was able to colonise in large numbers and dominate to almost the top of the *grossouvrei* Subzone in both localities, thus suggesting that conditions on the sea floor were perhaps less 'soupy' and suitable for burrowing. (This is reflected in the nature of the sediments; a change from bituminous shales to varying sediments at approximately the *obductum*-*grossouvrei* Subzonal boundary, see Figures 3.4 and 3.6) Around horizons 38-50 in Calvert pit, and horizons 26-40 in Saxon pit both infauna and epifauna occur, alternating in large numbers.

Thus during the *obductum* Subzone of the Peterborough Member (horizons 4-24, Calvert pit, and horizons 0-15, Saxon pit) the sea floor was relatively stable and in a 'soupy' condition, allowing *M. braamburiensis* to achieve large populations - up to 700 individuals per 200 mm x 1000 mm x 1000 mm square. At the start of the *grossouvrei* Subzone (horizon 24, Calvert pit, and horizon 17, Saxon pit), a significant change occurred to firmer substrates allowing infauna to colonise (seen by the presence of a nuculacean shell bed at both localities); however the rest of the *grossouvrei* and *phaeinum* Subzones (approximately horizons 25-52, Calvert pit and 16-49, Saxon pit) fluctuated between firmer substrates and softer substrates. It was probably due to these fluctuations that *M. morrisi* was not able to attain the large population sizes that *M. braamburiensis* exhibited in the lower part of the Peterborough Member.

At Orton pit the section is present up to the *obductum* Subzone only, due to removal of the higher subzones by glacial activity. Population numbers of the fauna match with Saxon pit over the *obductum* Subzone, with large numbers of *Meleagrinnella* (on average, over 80 per horizon, with a maximum of 196 in any one horizon) and only rare nuculaceans (never more than 8 per

horizon). Therefore the same conclusions reached for Saxon pit during this subzone can also apply to Orton pit.

6.3 Lithological evidence for environmental change

Previously the Peterborough Member has been described as predominantly organic-rich mudstones (Martill & Hudson 1991, p.20), however, numerous lithofacies and biofacies have been observed within the member. In Sections 4.2.5-4.2.7 Duff's biofacies were summarised in Tables 4.1-4.3, however, these are somewhat misleading because bed thicknesses were not represented. Here, Duff's (1975) biofacies are graphed against each bed number for Calvert and Saxon pits (Figures 6.2a and b).

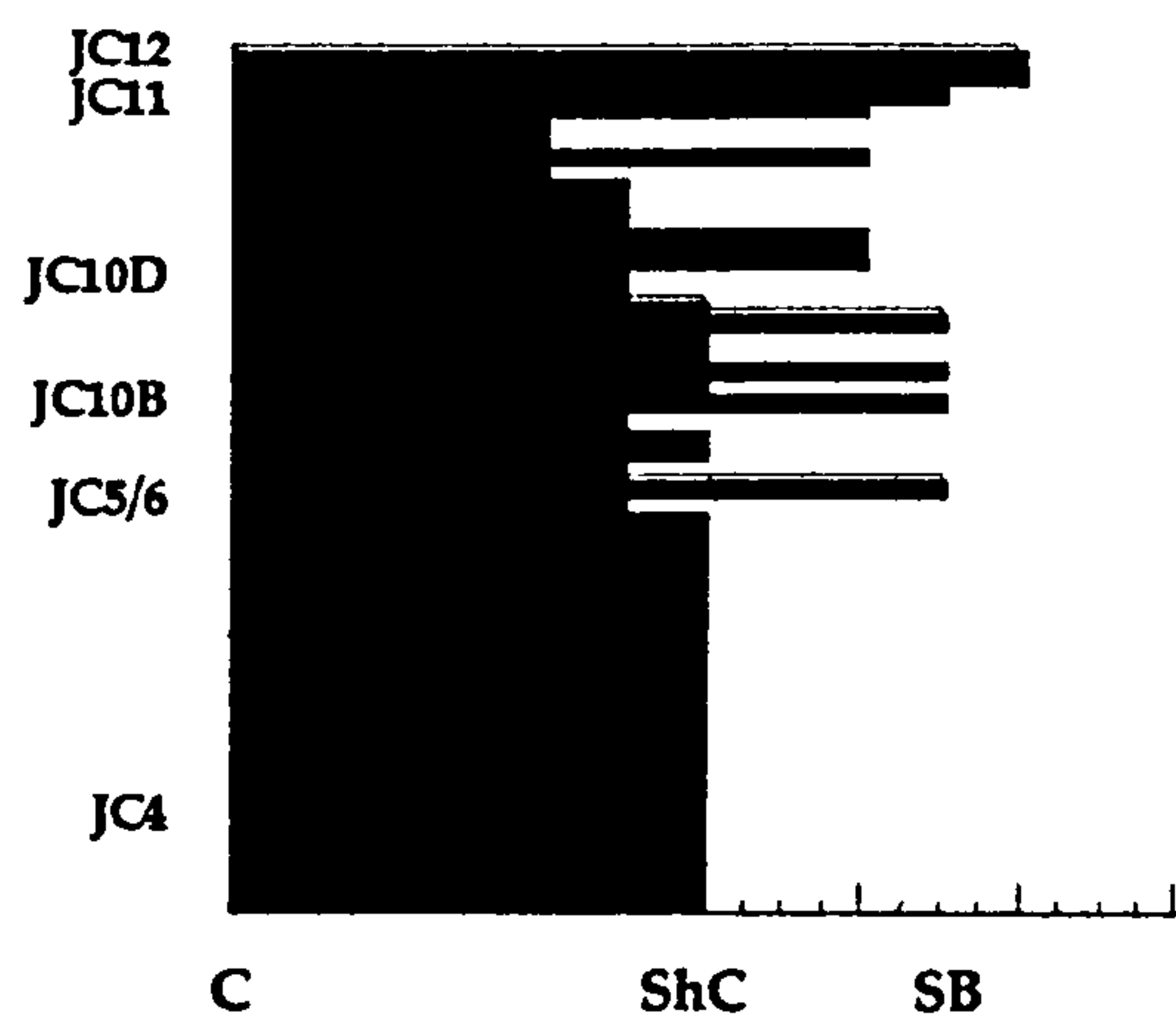


Figure 6.2a. Schematic graphic log for Calvert landfill site, Buckinghamshire.

C = clay, ShC = shaley clay and SB = shell bed, indicating increasing grain size from left to right across both figures. Note, not all bed numbers are displayed. (Bed JS14, Saxon pit is equivalent to bed JO14 at Orton pit).

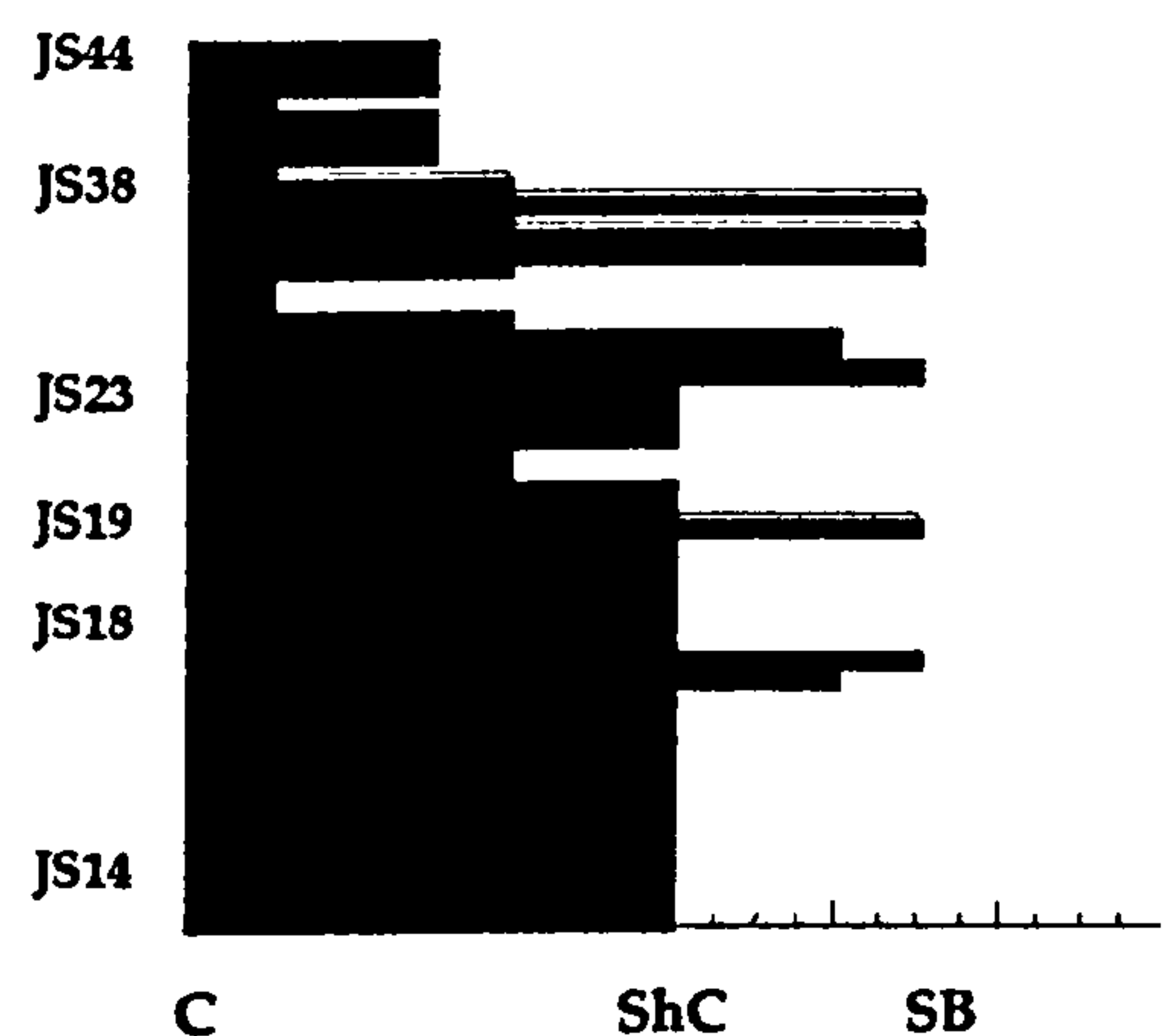


Figure 6.2b. Schematic graphic log for Saxon brick pit, Peterborough.

The schematic log of Calvert pit Figure 6.2a, illustrates the numerous lithologies within this pit. At the base of the section (bed JC3C) the lithology is continuous shaley clay through to bed JC4. After bed JC4 the lithology alternates between shaley clays, shales, and shell beds. Overall, Calvert pit has a period of similar lithology during the lower half of the deposition of the Peterborough Member, followed in the upper half by more dramatic fluctuating lithologies.

Figure 3.4 (see separate book of figures) provides a more detailed log of the section showing its different facies (facies after Duff 1975), whereas the schematic log (Figure 6.2a) illustrates the change in grain size of lithologies. Beds JC3C and JC4 are the same lithology and therefore represent more stable environmental conditions. Beds JC5-JC10B are thinner beds of distinctly different lithologies and represent more fluctuating environmental conditions. Beds JC10C and JC10D are two thicker beds of different types of bituminous shales and represent slight differences in environmental conditions between beds, with similar lithology throughout each bed. Beds JC10E through to bed JC12 are thin and represent rapidly changing lithologies.

Thus a More Stable Zone for environmental conditions (called the MSZ) at Calvert pit is represented by beds JC3C and JC4 (horizons 1-24) and a More Fluctuating Zone of environmental conditions (called the MFZ) is represented by beds JC5-JC12 (horizons 25-52). A period of slightly less fluctuating environmental conditions within the MFZ occurred during beds JC10C and JC10D (horizons 34-45).

Figure 6.2b, the schematic log of Saxon pit, also shows numerous different lithologies. However, instead of placing Duff's biofacies against the beds (Table 4.3), the variations that are represented in the log are more clearly delineated allowing an immediate appreciation of the lithology in Saxon pit.

The same type of lithology is present during bed JS14 (shaly clay; which is also equivalent to bed JO14 at Orton pit). Bed JS15 is a nuculacean shell bed horizon indicating a significant change in environmental conditions from the shaly clay below. This is followed by the same type of shaly clay (bed JS16), and above this another shell bed follows of nuculacean type (bed JS17), followed by a thicker bed (bed JS18) of bituminous shale. Above bed JS18, another nuculacean shell bed occurs (bed JS19) which is followed by similar dramatic changes in lithology: from shales, to shaley clays, to clays followed by shell beds, more shaley clays, shales and clays. The lithologies indicate more stable environmental conditions within the lower part of the pit (bed JS14) and fluctuating environmental conditions in the higher section (bed JS15 upwards). Figure 3.6 (see separate book of figures) shows each facies (facies after Duff 1975) and the changes in lithology above bed JS15. From bed JS24 to bed JS38 (Acutistriatum Bed) is the most fluctuating part of the MFZ, indicated by

very thin beds changing rapidly in lithology type. Above the *Acutistriatum* Bed (beds JS39-JS42) the lithology is of the same type - calcareous clay.

Therefore at Saxon and Orton pit the MSZ occurs during bed JS14 and bed JO14 respectively; bed JS15 marks a change in lithology at Saxon pit, which is distinctly different to that of the bituminous shales facies below. After this the lithologies fluctuate at Saxon pit, indicating changes in environmental conditions until bed JS38; above bed JS38 the lithology indicates more stable environmental conditions.

6.3.1 Summary

A distinct change in lithological types occurs at approximately the *obductum-grossouvrei* Subzonal boundary in both pits (top of bed JC4 at Calvert pit and top of bed JS14 at Saxon pit. In the lower part (the *obductum* Subzone) more stable environmental conditions are suggested by similar lithologies in all three pits, whereas within the upper part of the section (*grossouvrei* and start of *phaeinum* Subzones) a more fluctuating environment may have prevailed, as indicated by the rapid lithological changes that occur at both Calvert and Saxon pits.

6.3.2 Lithofacies analyses of the Peterborough Member

Macquaker's (1994) studies on the Oxford Clay found the majority of the Peterborough Member to be clay-rich mudstones. Macquaker's study was initiated to describe in detail some of the lithofacies present in the Oxford Clay Formation and to describe the main sedimentary factors that controlled the development of the mudstones, i.e. the environmental conditions under which they were deposited.

Stratigraphical relationships between some of the key components analysed by Macquaker are illustrated below (Figure 6.3):

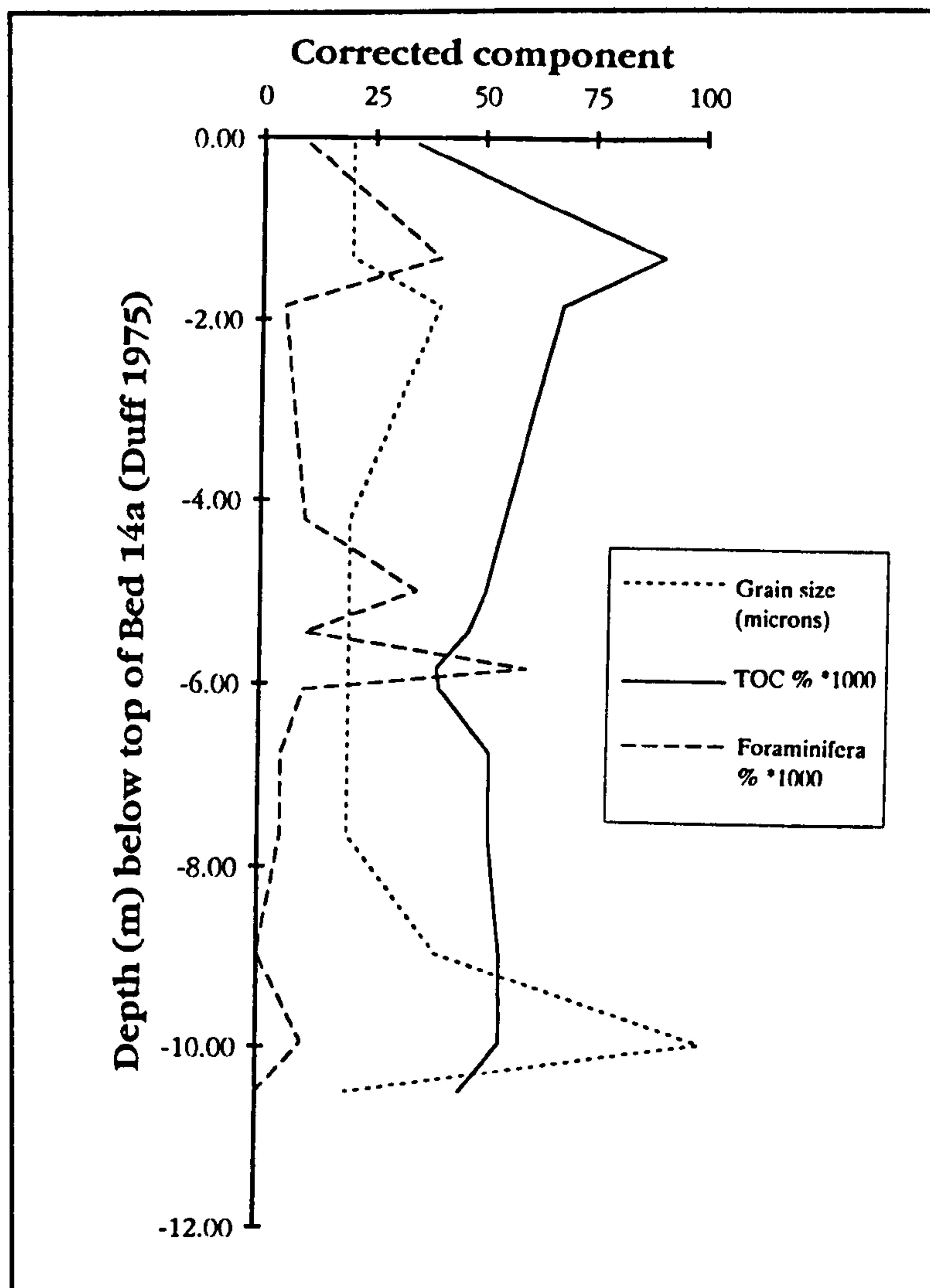


Figure 6.3. Log, after Macquaker (1994, p.171), illustrating the stratigraphic variations in TOC content, foraminifera abundance and grain size of the coarse detrital fraction. Depths taken below a datum defined as the top of bed 14a, Stewartby pit (Duff 1974). (-5.8 m is equivalent to the *obductum-grossouvrei* Subzonal boundary, with the *obductum* Subzone below, and the *grossouvrei* Subzone above.)

Macquaker (1994) argued that grain size variations observed in the succession reflected changes in the length of the sediment transport path through time. Two fining-upward successions and a coarsening-upward succession were recognised, although it should be noted that Macquaker based his observations on only 13 samples (Figure 6.3). The lower fining-upward succession was separated, at approximately -5.5 m, from the coarsening-upward succession by a bed composed of concretionary carbonate (equivalent to the concretionary carbonate layer of bed JC6, Calvert pit). This is approximately the same place in the sequence that the MSZ boundary with the MFZ boundary was placed in the previous discussion (Section 6.3).

Macquaker (1994) suggested that the concretionary carbonate between the two samples (S90-7 and S90-8, *obductum* Subzone, equivalent to the concretionary carbonates of bed JC6, Calvert pit), was formed close to the sediment-water interface as a consequence of sulphate reduction by bacterial processes. (Oxygen isotope data from Hudson 1978, p.357, suggest that the concretions grew within contact with the sea water; that burial can have been no more than 2 metres.) It is also known (Bottrell & Raiswell 1990) that these concretionary carbonates do not precipitate in continuously deposited sediments, but either where there is a break in sedimentation or during periods of very slow sediment accumulation.

Macquaker (1994) suggested that the formation of the concretionary carbonates occurred during a period of slow sediment accumulation at the inflexion point between fining and coarsening-upward successions and, that this was associated with the development of a condensed sequence during a period of high sea-level stand.

Foraminifera are abundant at two horizons (S90-7 and S90-9, top of *obductum* Subzone, -5.8 to -5.0 m). Recent benthic foraminifera tend to inhabit relatively stable environments, therefore Macquaker argues that these horizons were deposited under similar environmental conditions. At these levels the sediment accumulation rates were probably slow in comparison with other parts of the succession and the sediment at the sediment/water interface was hospitable. It is also likely that this part of the succession was deposited during a period when the bottom waters were well oxygenated (Macquaker 1994).

Similarly to Duff (1975) five types of lithology were found, petrologically, by Macquaker (1994): clay-rich mudstones, silt-rich mudstones, foraminifera-rich mudstones, concretionary carbonates and muddy sandstones. Clay rich mudstones occur throughout the whole of the *obductum* Subzone or lower half of the Peterborough Member. The clay-rich mudstones abundant in foraminifera also occur within the *obductum* Subzone, and indicate more stable environmental conditions. After the *obductum* Subzone a major change in environmental conditions occurred, marked by the presence of the concretionary carbonate. Major changes in lithofacies appear within the *grossouvrei* Subzone above and the *jason* Subzone below the *obductum*

Subzone, with silt-rich mudstones, shell beds, concretionary carbonates, and fine muddy sandstones. Within these two subzones changing lithologies, changing foraminifera content and varying TOC content occur (Figure 6.3). Note that between 0 and –6.00 m on Figure 6.3 the percentage of foraminifera changes greatly, but between –6.00 and –10.00 m there is much less variation (at –6.00 m the boundary between the *obductum* and *grossouvrei* Subzones occurs). The TOC data show more stability between –6.00 and –10.00 m, whereas between 0 and –6.00 m the TOC fluctuates. This indicates the *jason* and *grossouvrei* Subzones were more fluctuating in environmental conditions than the *obductum* Subzone.

6.3.3 Current lithofacies analysis of the Peterborough Member

Previously, changing lithofacies on the micro scale have been discussed (see Section 4.4 and Appendix 4). These changes have implications for interpreting the environmental conditions. Macquaker & Howell (in press) have argued that during the whole of the *obductum* Subzone and the base of the *grossouvrei* Subzone at Peterborough (beds JS14-JS18) there were changes in lithofacies between clay-rich, silt-rich mudstones and shell beds (JS15 & JS17). Results showed that six broadly upward-coarsening intervals (metre scale) could be detected; these had clay-rich bases coarsening up to silt-rich mudstones. Within the metre-scale upward-coarsening intervals remnant upward-fining couplets were observed (Plate A4.2), suggesting storm deposition as the main depositional mechanism.

Previously it has been assumed that beds JS14-JS17 (Figure 1.4) were ‘...the most uniform, part of the succession’ (Hudson & Martill 1994, p.119). The observed changes in lithofacies by Macquaker & Howell (in press) were therefore unexpected (see Plates A4.3-A4.8). Although Macquaker & Howell have observed some lithofacies change within beds JS14 & JS18 these are extremely small facies changes (just clay-rich to silt-rich mudstones) in comparison to the facies changes observed within beds JS15-JS17 (changes from coarse silt-rich mudstones to shell beds) (see Plate A4.8). Macquaker & Howell did not observe laminated mudstones, sandy mudstones, nannoplankton-rich mudstones or concretionary carbonates although these had previously been observed within the Peterborough Member (Macquaker 1994). These other

lithologies are confined to the rest of the *jason*, *grossouvrei* and *phaeinum* Subzones, where they are observed with shell beds, silt and clay-rich mudstones (Figures 1.4, 3.4, 3.6, and Figure 4 of Macquaker & Howell in press, see Appendix 4 for copy).

Figure 4 of Macquaker & Howell (in press) illustrates the six, broadly upward-coarsening successions, the lower three being not large enough changes in lithofacies to affect the fauna (see Figure 6.1b, up to horizon 16). Between the third and six upward-coarsening succession there are large changes in silt:clay ratio (from 0.1 to 0.22 to 0.13 to 0.18 to 0.01) (Plate A4.8) where a condensed upward-coarsening interval occurs and where faunal changes occur (see Figure 6.1b, above horizon 17). These large changes in silt:clay ratio indicate significant changes within the sediment deposited and large hiatuses. Previously researchers (e.g. Hudson & Martill 1991) have argued that there were significant hiatuses at the major shell beds with cryptic hiatuses elsewhere. Macquaker & Howell (in press) have indicated that major hiatuses occur between beds JS15, JS16 and JS17, and that the newly recognised parasequence boundaries (top of the upward-coarsening intervals) and bedding planes would be good candidates for the location of these cryptic hiatuses.

The major changes in silt:clay ratio between the third and six upward-coarsening interval coincides with the *obductum-grossouvrei* Subzonal boundary, which has already been suggested as the boundary between the MSZ and the MFZ. The dramatic change in silt:clay ratio gives more evidence for a change from more stable environmental conditions during the majority of the *obductum* Subzone and for more fluctuating environmental conditions above bed JS14.

Faunal evidence and lithofacies evidence coincides to suggest stable environmental conditions during bed JS14 (equivalent to horizons 0-24 Calvert pit and horizons 0-15 Saxon pit, see Figures 3.4, 3.6, 6.1a and b). Above bed JS14 both the lithofacies data (silt:clay ratio) and faunal compositions (see Figures 4 in Macquaker & Howell (in press) and 6.1a and b) change dramatically, and the lithofacies data stabilises once more during bed JS18. Unfortunately Macquaker & Howell (in press) did not analyse the sediment above this bed, therefore we can only assume that the silt:clay ratios will continue to change as the lithofacies change quite dramatically above bed JS18

(see Section 6.3.2). Faunal evidence (Figures 6.1a and b) indicates changes in composition above bed JS18 (horizon 20 upwards on Figure 6.1b). All the evidence suggests a relatively more fluctuating environment above bed JS14, at approximately the change from the *obductum* Subzone to *grossouvrei* Subzone.

6.4 Geochemical evidence for environmental change

The Oxford Clay has been previously well studied (see Journal of the Geological Society, London, 151 (thematic set of papers), 1994), by a number of authors to gain insights into its formation. These previous studies are used here as evidence of changes in environmental conditions within the Peterborough Member.

6.4.1 Biogeochemical evidence

Kenig *et al.* (1994) studied the isotopic biogeochemistry of the Peterborough Member, and included some samples from the underlying Kellaways Formation and overlying Stewartby and Weymouth Members.

The total organic carbon (TOC) data of the 165 samples analysed vary between 0.5 and 16.6 % by weight. Figure 6.4 shows TOC against bed numbers for Peterborough only; these are representative of Saxon and Orton brick pits.

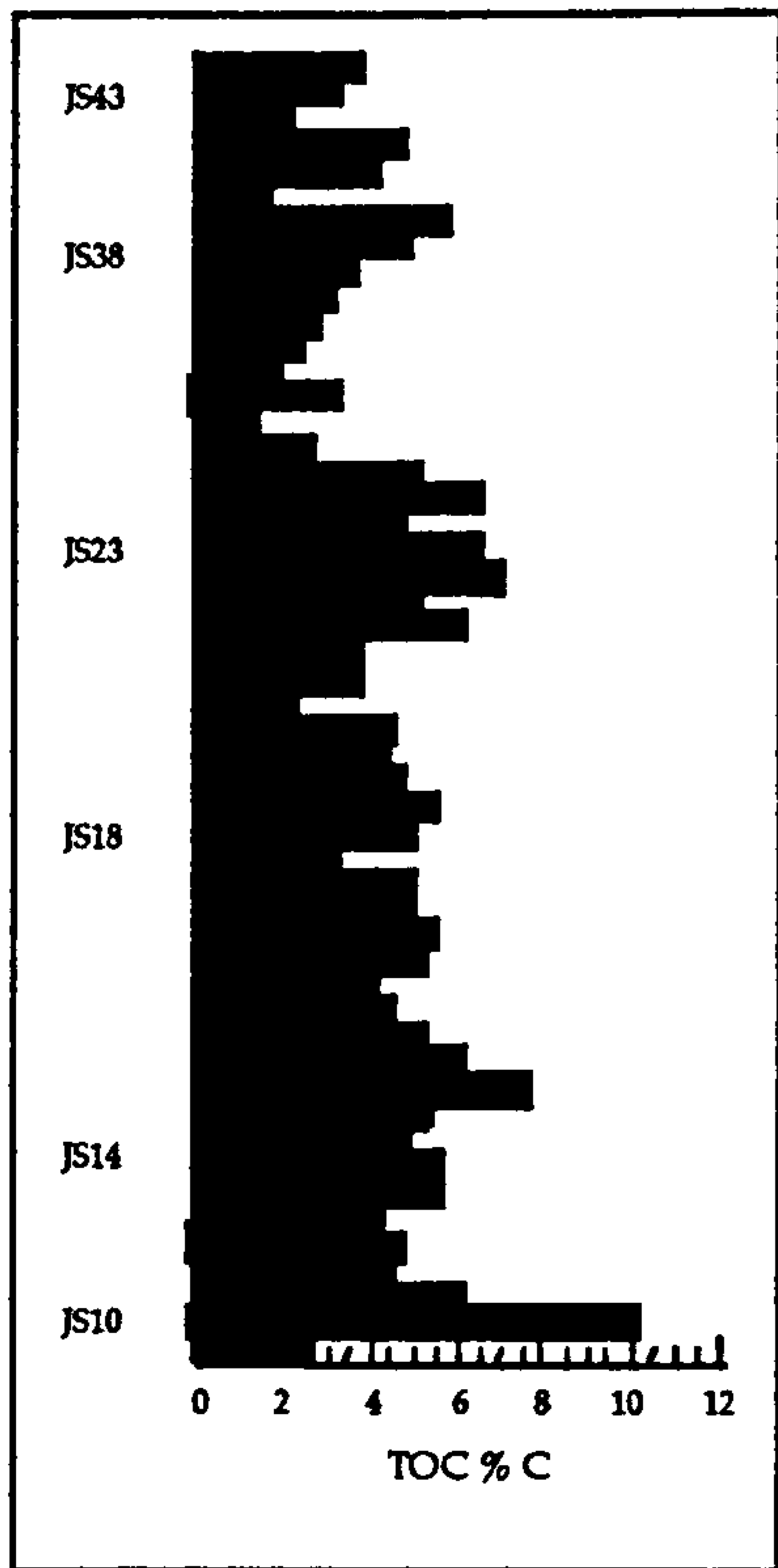


Figure 6.4. Total Organic Carbon (weight % TOC) data for Peterborough, modified from Kenig *et al.* (1994, p.143). Note only certain bed numbers are given on this figure.

The distribution of organic carbon within the Peterborough Member is heterogeneous. Bed 10 (Hudson & Martill 1994, p.118), at the base of the *jason* Subzone, is particularly organic rich. Figure 6.4 gives 10% TOC for this bed, but this bed can be up to 15% at some localities. Within bed 14 (Figure 6.4), the TOC varies, although not dramatically (between 3% and 8% maximum variation). However, from bed 18 onwards the variation within TOC appears to be more dramatic, with greater differences (between <2% and 8%). The greater fluctuations start just below bed 18 and continue up through the section. Unfortunately, there are no TOC data for beds 15, 16 and 17, as Kenig *et al.* (1994, p.143) did not analyse these beds. Presumably this is because beds 15 and 17 are nuculacean shell beds, composed almost entirely of shells with little sediment. However, a peak in TOC would be expected at beds 15 and 17, therefore the variations in TOC above bed 14 may be even greater than represented on Figure 6.4.

The hydrogen index (HI) (Figure 6.5a) was analysed by Kenig *et al.* (1994), in milligrams of hydrocarbon produced during pyrolysis per gram of organic carbon (HCg^{-1}C). High values ($\text{HI} > 500$) are representative of well preserved, thermally immature materials. The HI values observed by Kenig *et al.* (1994) from the Peterborough Member are high, averaging 553 $\text{mg HCg}^{-1}\text{C}$. This contrasts with values for the underlying Kellaways Formation and overlying Stewartby Member ($\text{HI} < 250$). Kenig *et al.* (1994, p.145) also suggested the great range of HI present within the Oxford Clay must have required significant chemical changes to be occurring. On the HI graph (Figure 6.5a) it is noticeable that the greater extremes or variations in HI are above bed JS18, with bed JS14 being relatively stable. Again Kenig *et al.* did not analyse beds JS15-JS17. This correlates well with both the palaeontological and lithological data which suggest that major changes in environmental conditions within the Peterborough Member occurred at approximately the *obductum-grossouvrei* Subzonal boundary.

The oxygen index (OI) (Figure 6.5b) was obtained by Kenig *et al.* (1994) from Rock-Eval pyrolysis (analyses giving different types of carbon within the sediment), and is given in milligrams of CO_2 produced per gram of organic carbon.

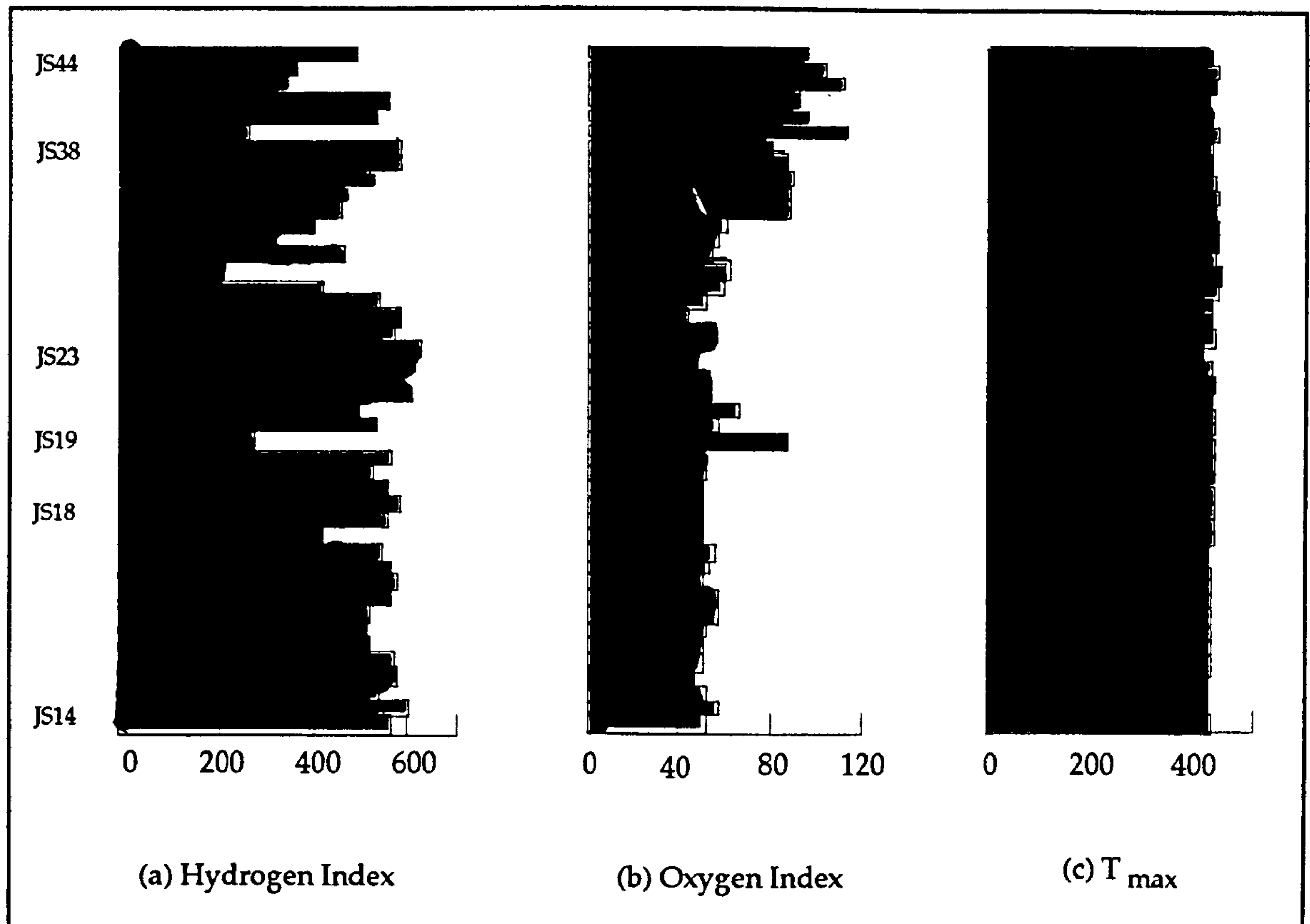


Figure 6.5. (a) Hydrogen index, (b) oxygen index, and (c) T_{\max} for Peterborough; data from Kenig *et al.* (1994, p.143). Note only certain bed numbers are given on these figures.

OI is an indicator of the amount of oxygen content of the organic matter. HI vs. OI was plotted by Kenig *et al.* (1994, p.145) in which H/C is plotted as a function of O/C (Figure 6.6). The results show clusters of groups. Deposit feeder shales (group A) are the dominant biofacies type (Duff 1975); these plot in the region of immature Type II organic matter. The bulk of the organic matter is of marine, phytoplanktonic origin (as defined by Espitalie *et al.* 1977; 1986). The high HI (500-800) of samples in this group indicates good preservation and low thermal maturity of the organic matter. Groups B1 and B2 are samples of *Gryphaea* shell beds and nuculacean, *Grammatodon* and mixed shell beds, respectively. The findings for the Oxford Clay indicate that deposit feeder shales were deposited under less oxic conditions than shell beds. This is consistent with the conclusions reached from analyses of bio-assemblages by Duff (1975). The deposit-feeder bituminous shales are the dominant lithology deposited during the *obductum* Subzone (bed JS14, Figure 1.4), with shell beds becoming much more dominant at the end of the *obductum* Subzone and in the *grossouvrei* Subzone. Thus less oxic (dysoxic) conditions prevailed during

most of the *obductum* Subzone when *M. braamburiensis* dominated (Figure 6.1a & b) (horizons 0-17), and generally more oxic conditions occurred during the *grossouvrei* Subzone when *M. morrisi* dominated (horizons 17-50).

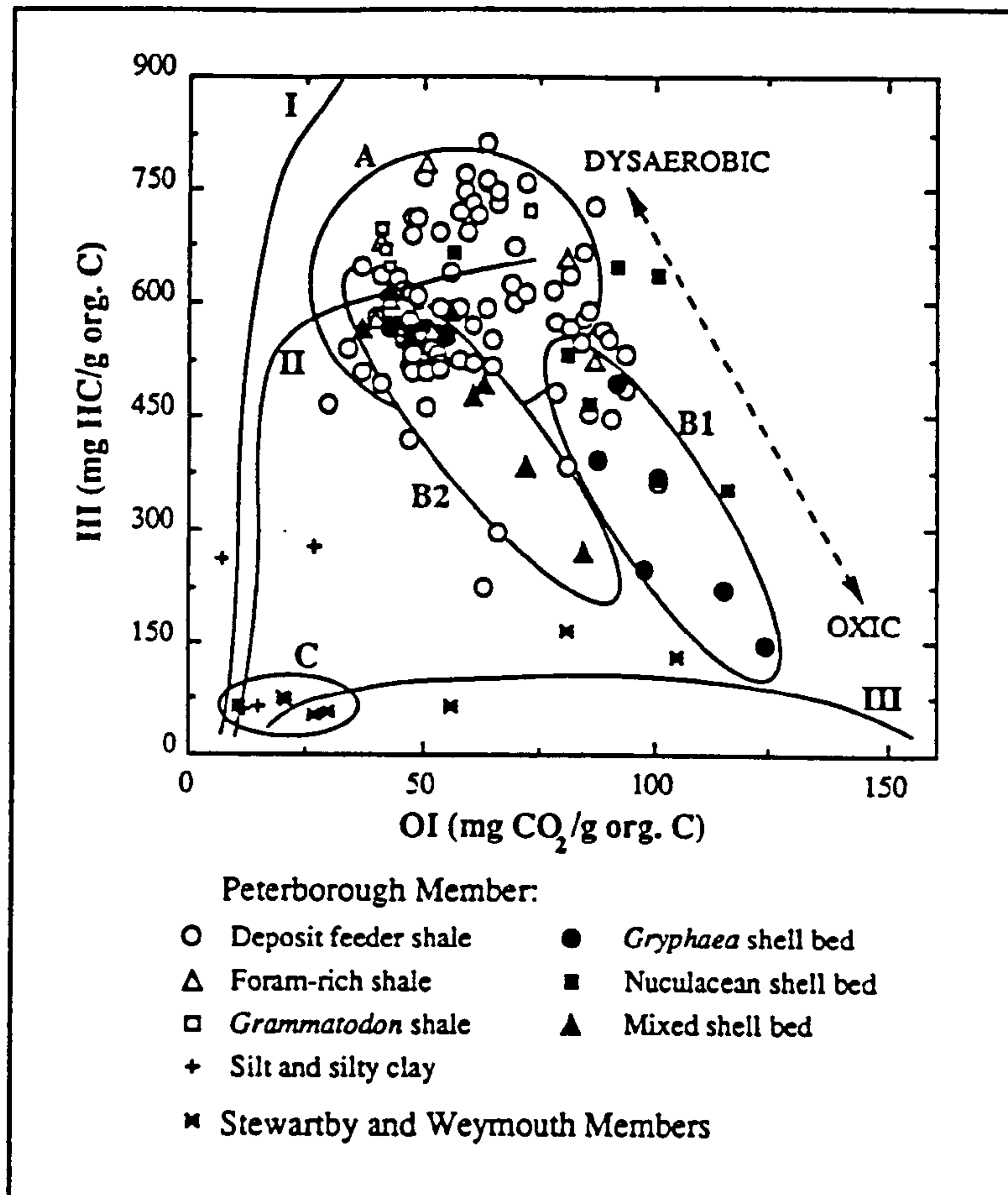


Figure 6.6. Plot of hydrogen index (HI) v. oxygen index (OI) (from Kenig *et al.* 1994, p.145).

The Oxford Clay has always been thought to be thermally immature (Hudson 1978), and this is confirmed by Kenig's *et al.* T_{\max} data (Figure 6.5c), which averaged at 419 °C for all the shale samples. This is a value well below the threshold of oil generation (≥ 435 °C) for organic matter of this type.

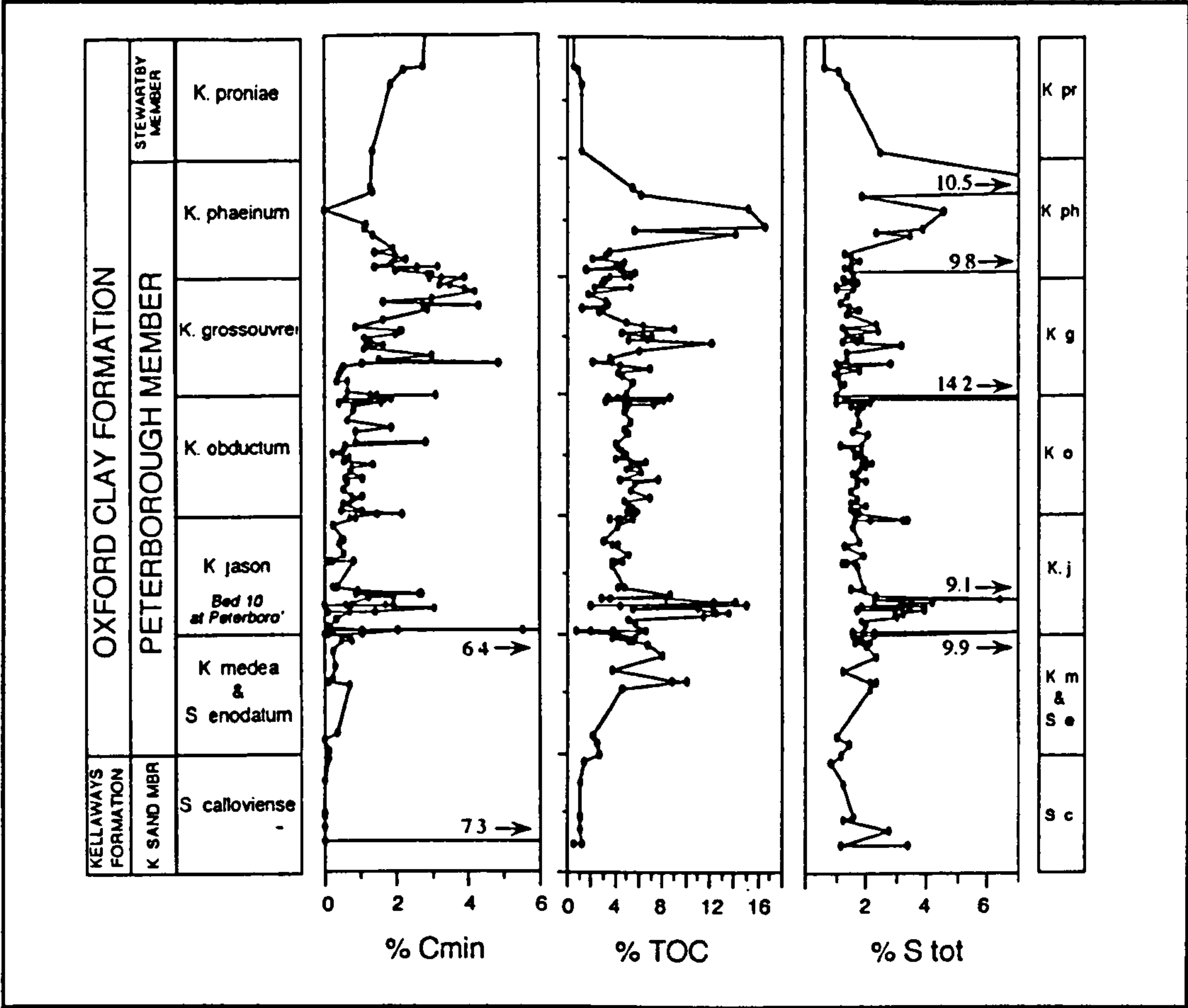


Figure 6.7a, band c. Bulk geochemical parameters obtained on whole-rock samples plotted versus time. Figure 6.7a, carbonate carbon (wt % C_{min}); Figure 6.7b, total organic carbon (wt % TOC); and Figure 6.7c, total sulphur content (weight % S) from Kenig *et al.* (1994, p.144).

Kenig *et al.* (1994) also analysed mineral carbon (Figure 6.7a) and found, on average, that shell beds contained more carbonate (2.1%) than the shales (1.0%). This is thought to be due to carbonate supplied by shells, which become more concentrated due to winnowing and slow accumulation rates. More shell beds occur within the *grossouvrei* and *phaeinum* Subzones than within the *obductum* Subzone (bed JC5 and above in Calvert pit and bed JS15 and above in Saxon pit, see Figures 3.4 and 3.6 respectively). The pattern of mineral carbon reflects this; there are more peaks of carbonate in the *grossouvrei* and *phaeinum* Subzones than within the *obductum* Subzone, again reflecting greater changes in environmental conditions within the *grossouvrei* Subzone than the underlying *obductum* Subzone.

The overall trend of increasing carbonate within the Peterborough Member was thought to be the result of increasing concentrations of coccoliths. This reflects a continuing marine transgression, increasing the distance to the

siliciclastic source and providing a more open marine environment, favourable to growth of coccolithophorids (Kenig *et al.* 1994, p.146).

The total sulphur content (Figure 6.7b) shows large variations, with the peaks of total sulphur related to changes in facies, specifically the presence of shell beds. Shell beds often mark subzonal boundaries, which are preferentially pyritised, thus sulphur contents are often more than 7% in these shell beds, which mark the subzonal boundaries. Note the large peak between the *obductum-grossouvrei* Subzones. Within the *obductum* Subzone, sulphur is relatively stable at approximately 2%, whereas in the *grossouvrei* and *phaeinum* Subzones considerable variation of sulphur content occurs, not just at subzonal boundaries.

Total organic was found to range between 0.5 and 16.6% by weight within the Peterborough Member (Figure 6.7c). Enrichment of ^{13}C occurs within bed 10 of the Peterborough Member; however ^{13}C decreases steadily throughout the *grossouvrei* Subzone, before rising rapidly in the *phaeinum* Subzone. These variations were thought to be due to environmental or biological effects in the marine palaeoenvironment (see Kenig *et al.* 1994, pp.146-149). Kenig *et al.* (1994, Figure 4, p.146) plotted the hydrogen index against δ_{TOC} which showed that the deposit-feeder shales varied in δ_{TOC} in response to variations in heterotrophy; because decreases in HI reflect oxidation of organic matter, heterotrophy might be related to loss of hydrogen. Variation of primary δ values appear to have been minimal during deposition of the shell beds (Kenig *et al.* 1994, p.150). Observed values of δ_{TOC} within the shell beds were found to be indicative of secondary isotopic fractionation in the same range observed in the Greenhorn Formation (Hayes *et al.* 1989, 1990) and in most samples from the Peterborough Member.

Kenig *et al.* (1994, p.150) thought variations in geochemical parameters occurred at two levels; one correlating with boundaries of ammonite subzones and reflecting hiatuses and large-scale changes of environmental conditions; other variations they suggested corresponded to biofacies recognised by Duff (1975) on the basis of macrofaunal assemblages. These major changes across subzonal boundaries were also observed within the population study (Section 6.2.2). Over the *obductum-grossouvrei* Subzonal boundary there is a distinct

change in facies (see Tables 4.1 and 4.3) reflected in the faunal composition (see Figure 6.1a and b) and geochemical parameters investigated by Kenig *et al.* (1994).

Kenig *et al.* (1994) showed that the depositional environment governs the bio-assemblage composition and influences the chemical composition of sedimentary organic matter. Deposit-feeder bituminous shales were interpreted to be deposited under dysaerobic conditions, which were more organic-rich and more hydrogen rich than shell beds, which were interpreted as deposited under aerobic conditions.

Kenig *et al.* (1994) showed important geochemical data which have been used to detect changing environmental conditions within the Peterborough Member. The graphed data (Figures 6.5-6.7c) show larger variations in the geochemical parameters investigated within the *grossouvrei-phaeinum* Subzones (beds JS15-JS44, Saxon pit (bed JS15 actually represent the top of the *obductum* Subzone) and beds JC5-JC12, Calvert pit) relative to more stable variations in geochemical parameters observed within the *obductum* Subzone (bed JS14 Saxon pit, and beds JC3C-JC4 Calvert pit).

6.4.2 Petrographic analyses

Belin & Kenig (1994) discussed the significance of organic matter within the Peterborough Member: all samples contained a high proportion of amorphous organic matter. However, the structural organic matter (SOM) increased proportionally with decreasing total organic matter, see Table 6.1 (Belin & Kenig 1994, p.157). Note how SOM increases consistently up through the Peterborough Member, and TOC decreases upwards through the Member. This suggests that conditions generally became more oxic through the member following more dysoxic conditions at the start, as suggested by high TOC.

Sample	Equivalent to bed No. in Saxon pit	TOC	HI	AOM %	SOM %	Observations
P89-13	10	14.2	813	95	5	Cuticle fragments and lignitic debris
P90-1	10	12.2	710	90	10	Cuticle fragments and lignitic debris
B89-7	12	5.6	661	85	15	Cuticle fragments and lignitic debris
C89-20	38	5.2	659	85	15	Cuticle fragments: 5-10% lignitic debris >5%
P89-22	12	3.8	222	80	20	Dominance of lignitic debris minor cuticle fragments
B89-17	Stewartby Member	1.2	130	75	25	Lignitic debris; numerous coaly, small-sized particles

Table 6.1. Characteristics of palynofacies, after Belin & Kenig (1994, p.157).

Belin & Kenig (1994) compared the hydrogen index and oxygen indexes obtained by Kenig *et al.* (1994) and confirmed that the chemical variations were related to oxygen content in the water column and at the sediment/water interface.

Belin & Kenig (1994) agreed with Kenig *et al.* (1994) that the deposit-feeder bituminous shales were deposited in more dysoxic environmental conditions whilst the rest of the Peterborough Member was deposited in more oxic environmental conditions. The deposit-feeder bituminous shales are beds JC4, JS14 and JO14, Calvert, Saxon and Orton pits respectively, i.e. the MSZ. These beds are followed in Calvert and Saxon pits by numerous alternating lithofacies, including shell beds known to be deposited in more oxic conditions.

6.5 Summary

Within this chapter changing environmental conditions within the Peterborough Member have been detected, using palaeontological, lithological and geochemical data.

The data suggested numerous distinct changes in environmental conditions within the Peterborough Member. The most visible changes are: the presence/absence of shell beds; these represent the most dramatic changes within the Peterborough Member. Shell beds are either winnowed horizons, or represent periods of non-deposition. There are numerous shell beds within the Peterborough Member, mainly restricted to the *jason*, *grossouvrei* and *phaeinum* Subzones. Other changes include: the sudden abundance of fauna, particularly nukulaceans (*M. morrisi*); lithological data indicating a sudden change to high silt:clay ratios; and geochemical evidence showing peaks of sulphur, carbonate carbon, TOC, HI and OI.

The Peterborough Member can be split grossly into two sections, a More Stable Zone (MSZ) of environmental conditions and a More Fluctuating Zone (MFZ) of environmental conditions.

The MSZ occurs in the lower part of the section, broadly the *obductum* Subzone (beds JC3C and JC4, horizons 0-24 at Calvert pit; bed JS14, horizons 0-15 at Saxon pit; and bed JO14, all horizons investigated at Orton pit). Both *M. morrisi* and *M. braamburiensis* bivalve lineages are present through this MSZ, although *M. braamburiensis* dominates this zone in all three pits. Lithological evidence indicates that the same lithofacies occurs throughout the MSZ in the Peterborough Member - bituminous shale-rich mudstone (Tables 4.1, 4.2 & 4.3). Geochemical data show less variation generally during this zone of the Peterborough Member.

The MFZ occurs in the upper part of the section, i.e. the *grossouvrei* and *phaeinum* Subzones (bed JC5 and above, horizon 25 onwards at Calvert pit; bed JS15 and above, horizon 16 onwards at Saxon pit). Both bivalve lineages dominate alternately (see Figure 6.1a and b). The lithology during the *grossouvrei* and *phaeinum* Subzones is variable, with silt-rich mudstones, clay-rich mudstones, sand-rich mudstones, shell beds, and concretionary carbonates (Figure 1.4). Geochemical evidence for the MFZ (illustrated in

Figures 6.5-6.8 and Table 6.1) indicates much more variation within every chemical parameter discussed in Section 6.4 during this part of the Peterborough Member than the MSZ below.

Thus the Peterborough Member records both relatively stable and fluctuating environments conditions, with the split being found at approximately the boundary between the *obductum* and *grossouvrei* Subzones. This is approximately horizons 0-24 (MSZ) and horizons 25-52 (MFZ) at Calvert pit; horizons 0-15 (MSZ) and horizons 15-49 (MFZ) at Saxon pit. The section of Peterborough Member at Orton pit only contains the *obductum* Subzone due to removal of the upper subzones by glacial activity; this corresponds to the MSZ.

CHAPTER 7

DATA & INTERPRETATION

The main aim of this study was to investigate microevolutionary patterns in bivalves obtained from differing environmental conditions during deposition of the Peterborough Member. Four variates were measured (Length, Height, Anterior Length, & Hinge Length) in order to examine possible microevolutionary patterns. The observed patterns were compared across the three different localities investigated. The Density of Ribs of *M. braamburiensis* was also calculated. Comparisons of data obtained in this study with Brinkmann's (1929) work were also carried out.

7.1 Growth patterns

Patterns of growth must be investigated to make sure that any shape changes which might be interpreted as evolutionary are true shape changes. Growth within the four measured variates can be either isometric or allometric.

Isometric growth occurs when, as one variate increases, the other variate increases at the same rate, so that any ratio of the two variates is always the same, no matter what the size of the individual. If growth is isometric, then any significant shape change (i.e. a significant change in ratio) within the lineage would be considered a true shape change. However, if the growth pattern is allometric, then as one variate increases the other increases at a different rate, creating a shape change as the individual grows. The ratio between the two variates is often never the same. If this is the case, a shift in ratio, even if significant, may not be a true shape change; it may just be an expression of sampling from a different place along the allometric growth curve. For further discussion on isometric and allometric growth see Skelton (1993, pp.477-485). Therefore, before any patterns are presented it is crucial to determine what type of growth the two studied lineages possess.

To determine whether growth is isometric or allometric, one must first plot a bivariate scatter graph to show the relative growth of two variates (Figure 7.1). A best-fit line is then fitted to the scatter plot to show the line of relative growth for the whole sample. If the growth is allometric, the best fit line conforms to the general allometric equation:

$$y = bx^a \quad (1).$$

If a is greater than 1 (positive allometry) the line of slope will gradually steepen, and if a is less than 1, the slope will gradually decrease upwards (negative allometry); $a = 1$ for isometric growth (see Figure 7.2). To produce a best-fit line or Reduced Major Axis (RMA) to the data and Figure 7.1, the following procedure was carried out (after The Open University 1993):

- All measurements were converted to logarithms.
- The mean of each variate was then calculated (mean of $\log L$, mean of $\log H$ for the Length against Height bivariate scatter plot and the same for the Hinge Length against Anterior Length bivariate scatter).
- The standard deviations (σ) were then calculated for each logged variate.
- The correlation coefficient (r) between the two variates, i.e. between the Length and Height, and the Hinge Length and Anterior Length, were calculated

converting the equation $y = bx^a$ to logarithms gives:

$$\log y = \log b + a \log x \quad (2).$$

The RMA of the logarithmic data passes through the point corresponding to the mean $\log x$ and mean $\log y$. The slope of the RMA, a , is given by the ratio of the sample standard deviations, σ_y/σ_x for the log values. The only unknown in the equation is $\log b$, which can be calculated from:

$$\log b = \text{mean} \log y - a(\text{mean} \log x) \quad (3).$$

The RMA was constructed using the following procedure:

- The points corresponding to the means of the logs (for the two variates) were marked. A straight line of slope a was drawn through this point. The line was extended to the y axis at $\log x = 0$
- Alternatively, one can mark the calculated value of $\log b$ on the y axis and draw a line between this point and the point for the means of the logs.

To be able to check to see whether the line is significantly different from 1, i.e. growth is allometric, the following equation is needed:

$$Z = a - 1/s_e \quad (4).$$

$$\text{Where } s_e = a\sqrt{1 - r^2/n} \quad (5).$$

From our previous workings we know a and r ; n is the sample size.

Here my null hypothesis was ' a does not significantly differ from 1.' To reject the null hypothesis, at the 0.05 (95%) level, Z must be equal to or greater in magnitude than ± 1.96 . If Z exceeds ± 1.96 then growth is said to be allometric, whereas if Z is less than ± 1.96 then growth is said to be isometric.

7.1.1 The five types of growth pattern

7.1.1.1 True isometric growth

In isometric growth (Figure 7.3) any point along the growth curve will have the same ratio. Any change in ratio as the lineage is followed through time will be due to a change in shape, not due to growth; if that change is considered to be significant then it is a real shape change. Thus if growth is true isometric growth ($a = 1$) one can just simply graph the two variates as ratios and usually detect any morphological changes. Morphological changes are detected by using a Student's t -test. A t -test will show if there is a significant difference between two samples (in this case two adjacent mean ratios) at the 95% confidence level ($P = 0.05$). The null hypothesis in this test would be 'the samples along this isometric curve are from the same population', i.e. have no differences. If the change in ratio is found to be significant then there is a shape or morphological change.

7.1.1.2 Allometric growth with 2 samples on the same growth curve, with different ratios

Figure 7.4 illustrates an example of allometric growth with two samples on the same growth curve but with different ratios. The ratios are different because of the allometric exponent; the lineage allometrically changes shape as it grows along the curve. However, even if the two samples are considered to be significantly different, they do not show any real shape change as they are on the same growth curve, and therefore the two different samples are just evidence of sampling at a different place along the same growth curve.

7.1.1.3 Allometric growth with two samples on different growth curves with the same ratio

Figure 7.5 illustrates an example of allometric growth with two different growth curves with two samples having the same ratio. The two samples here have been determined as being from two separate allometric growth curves. The fact that the two samples have equal mean ratios suggests little chance of a significant shape change as a t-test would not pick out any difference in the mean ratio. However, growth curves can still be significantly different to each other.

7.1.1.4 Allometric growth with 2 samples on different growth curves, with different ratios

Figure 7.6 illustrates two samples that have been determined as being from two populations with different growth. The two ratios are different; this shape change could be considered as a true shape change if the two ratios are found to be significantly different using the t-test, as they have been found to come from populations with different allometric growth curves.

7.1.1.5 All growth styles

Figures 7.3-7.6 illustrate all the different types of growth and relationships of mean values that could occur within a data set such as that of the present study. Therefore, as long as the growth type is determined to be isometric the four variates can be graphed as ratios, and true shape changes can be detected by determining whether the samples are significantly different from one another. (This will be carried out using a t-test). Therefore if a shape change occurs with isometric growth then this is considered to be a true shape change. If the growth type is determined to be allometric, the samples can still be graphed as ratios, however, t-tests cannot be applied unless the samples are standardised for size. Within this study the samples have not been standardised for size and therefore t-tests were not applied to these samples. However, allometric samples found to be from populations with different allometric growth curves, are considered to show a change in the pattern of growth, and therefore represent a shape change. Allometric samples found to lie on the same growth curve do not show any change in the pattern of growth, and are therefore considered not to show any sort of shape change.

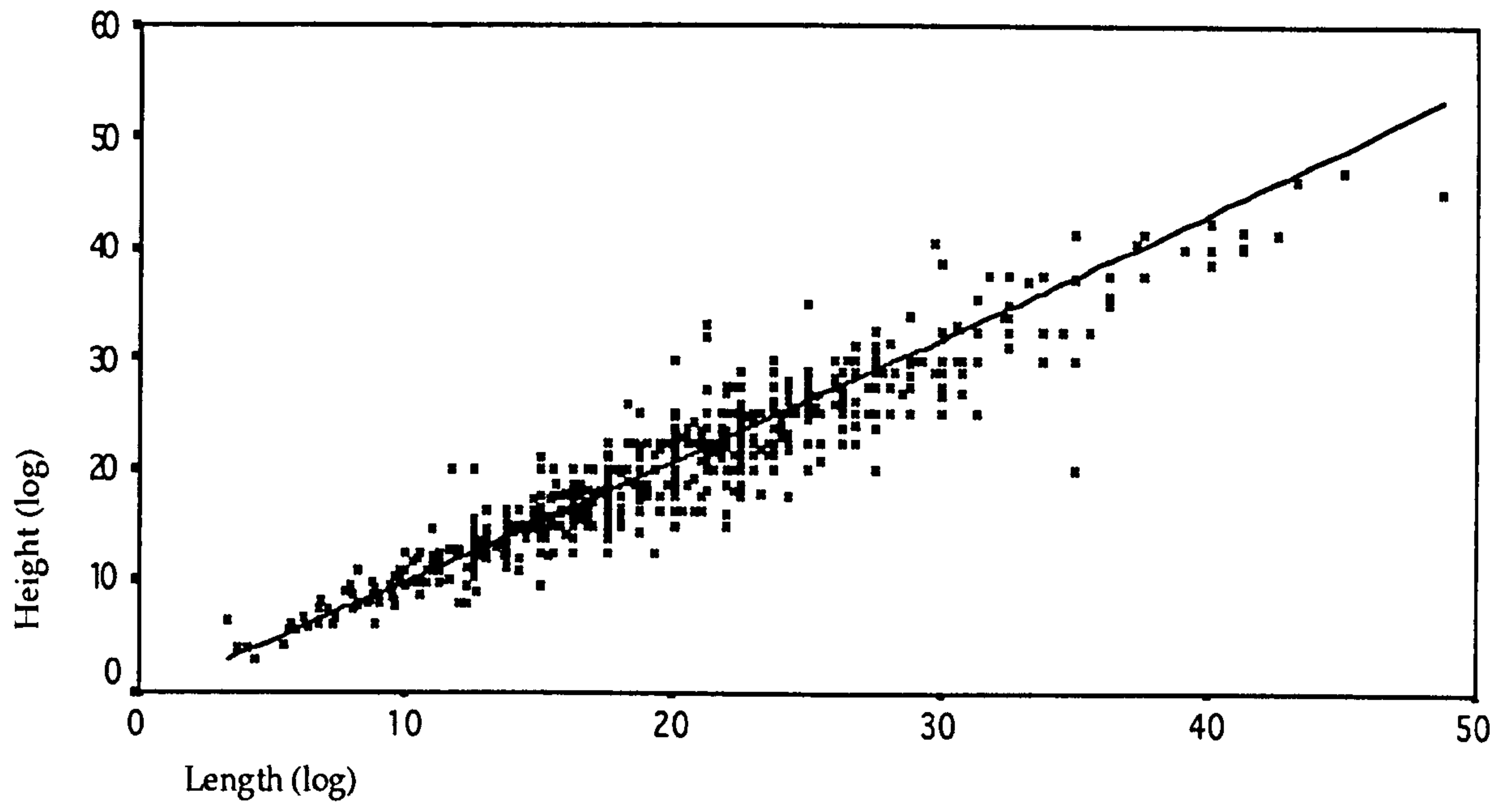


Figure 7.1. An example of a bivariate scatter plot for a bivalve, see text for further discussion.

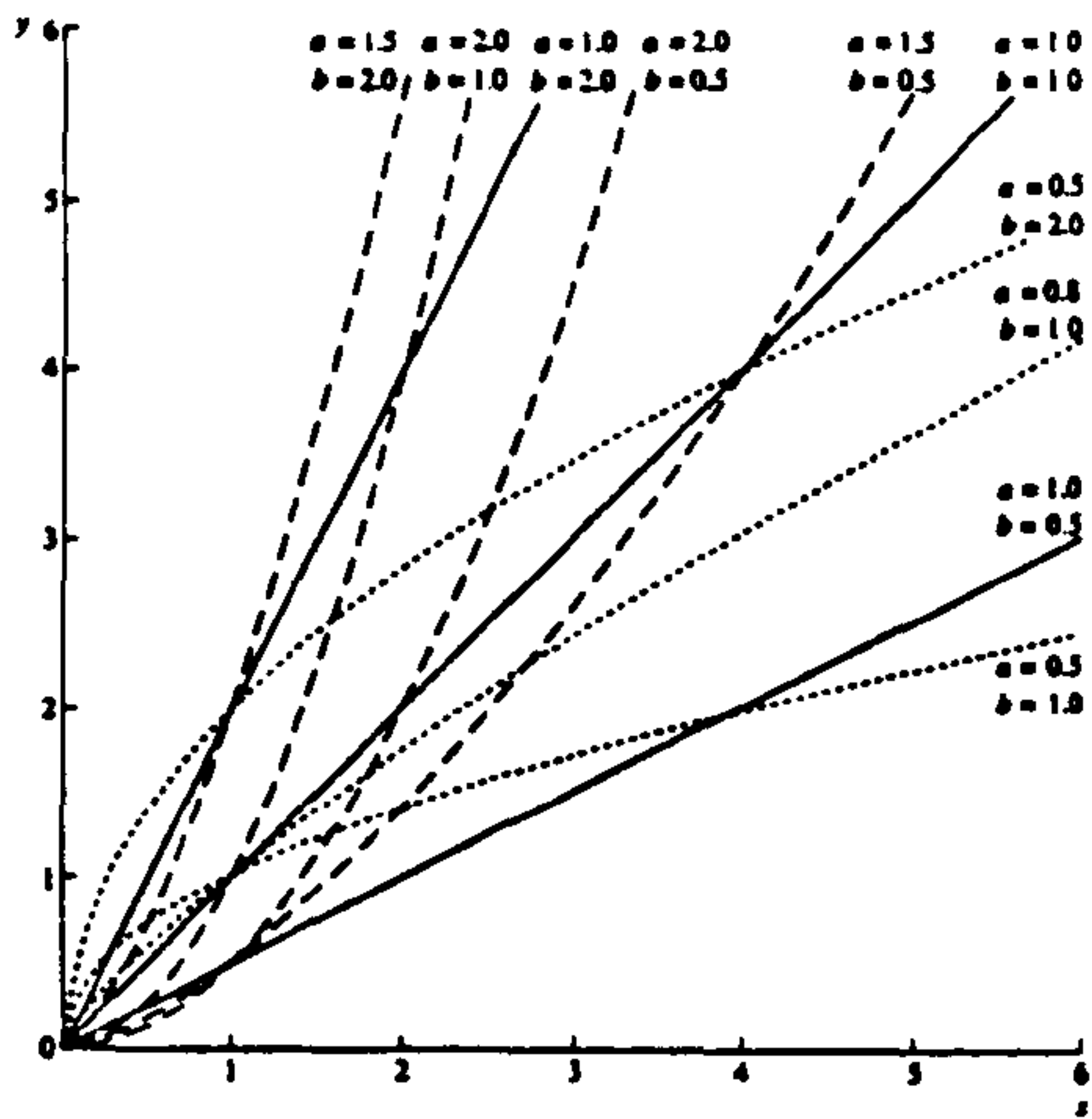


Figure 7.2. Various lines of relative growth, each of the form $y = bx^a$ (from Open University 1993).

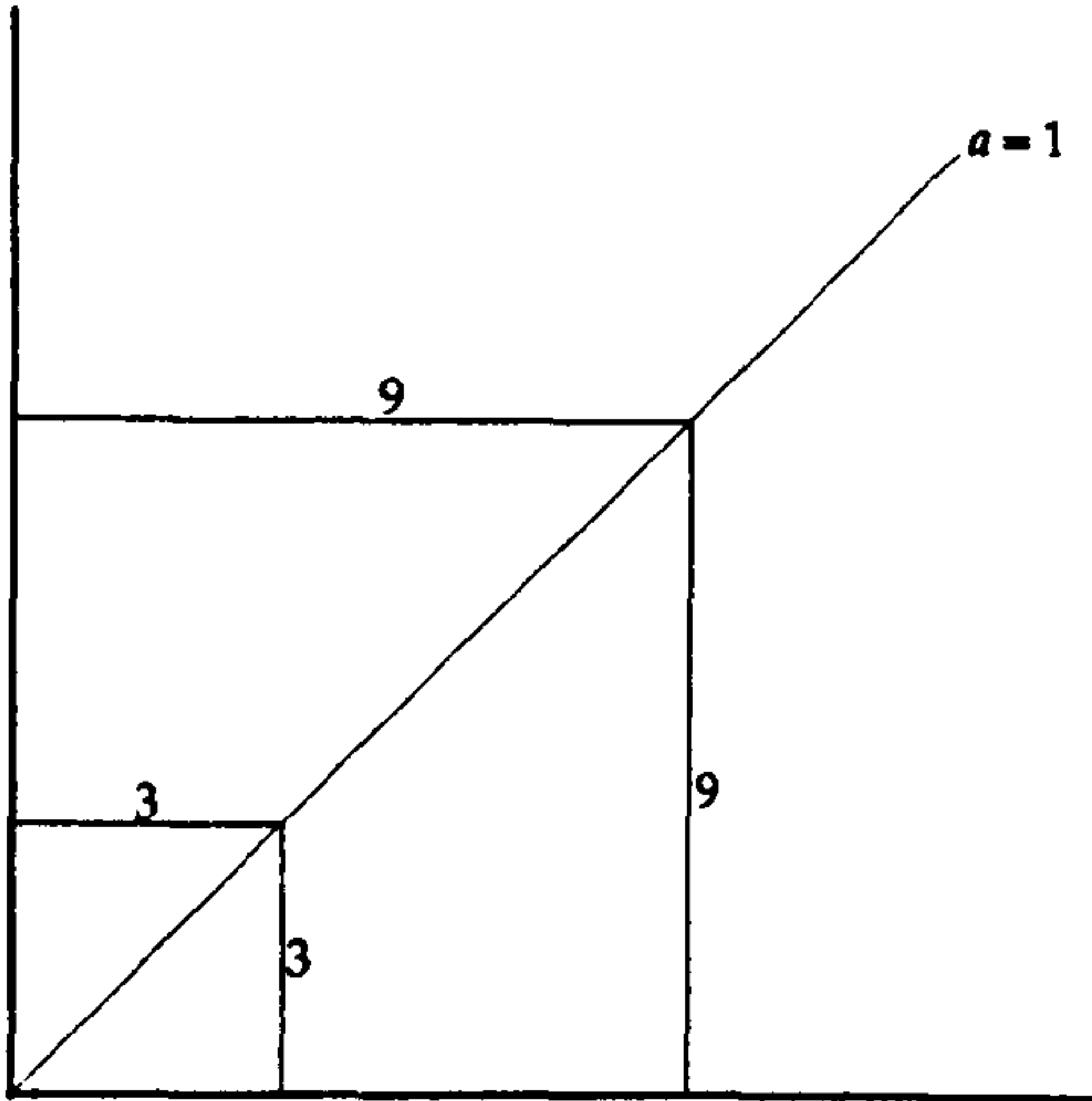


Figure 7.3. Isometric growth, where the ratio is always the same: $3/3 = 1$; $9/9 = 1$.

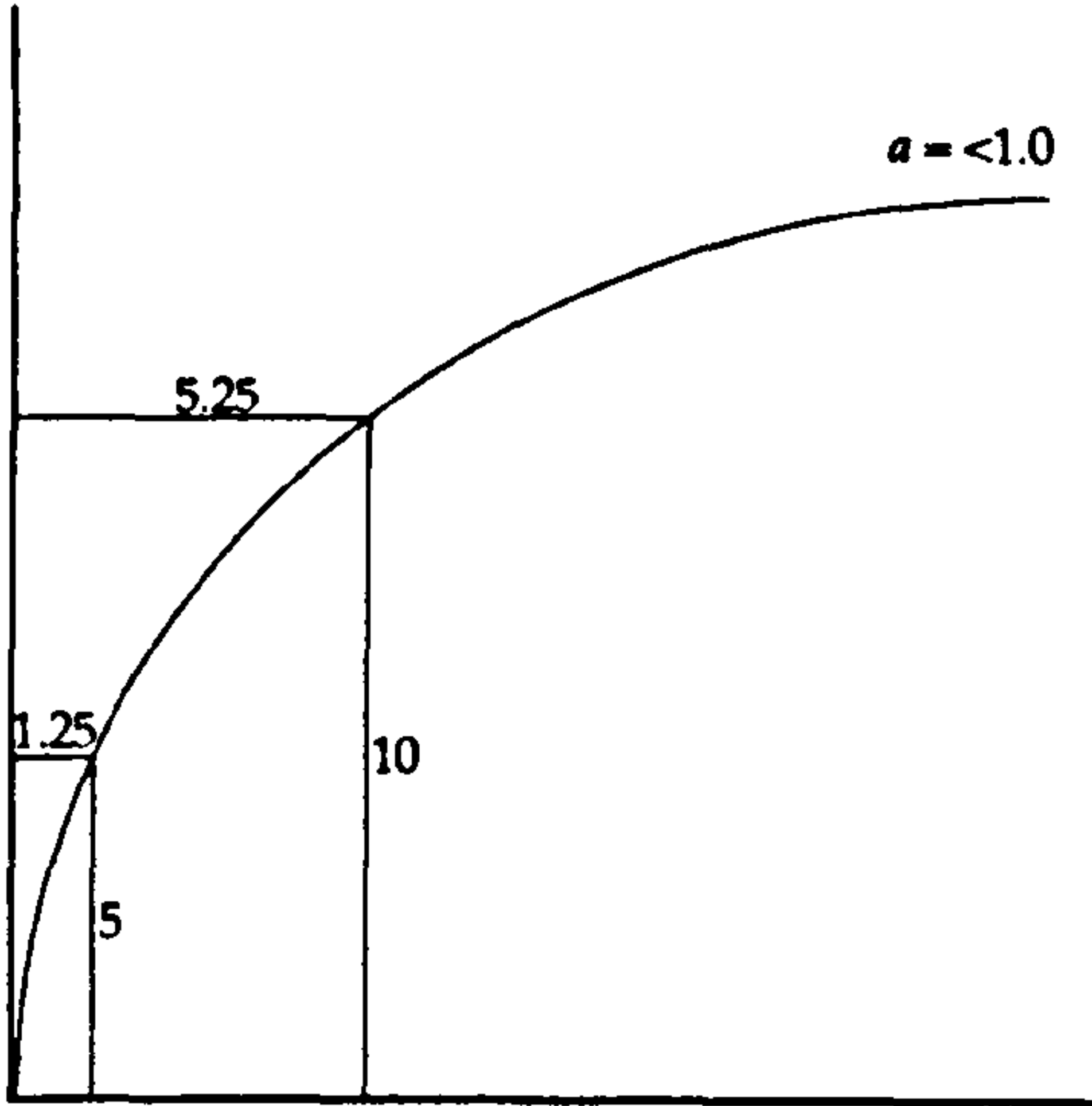


Figure 7.4. Allometric growth with 2 means on the same growth curve, with different ratios: $1.25/5 = 0.25$; $5.25/10 = 0.52$.

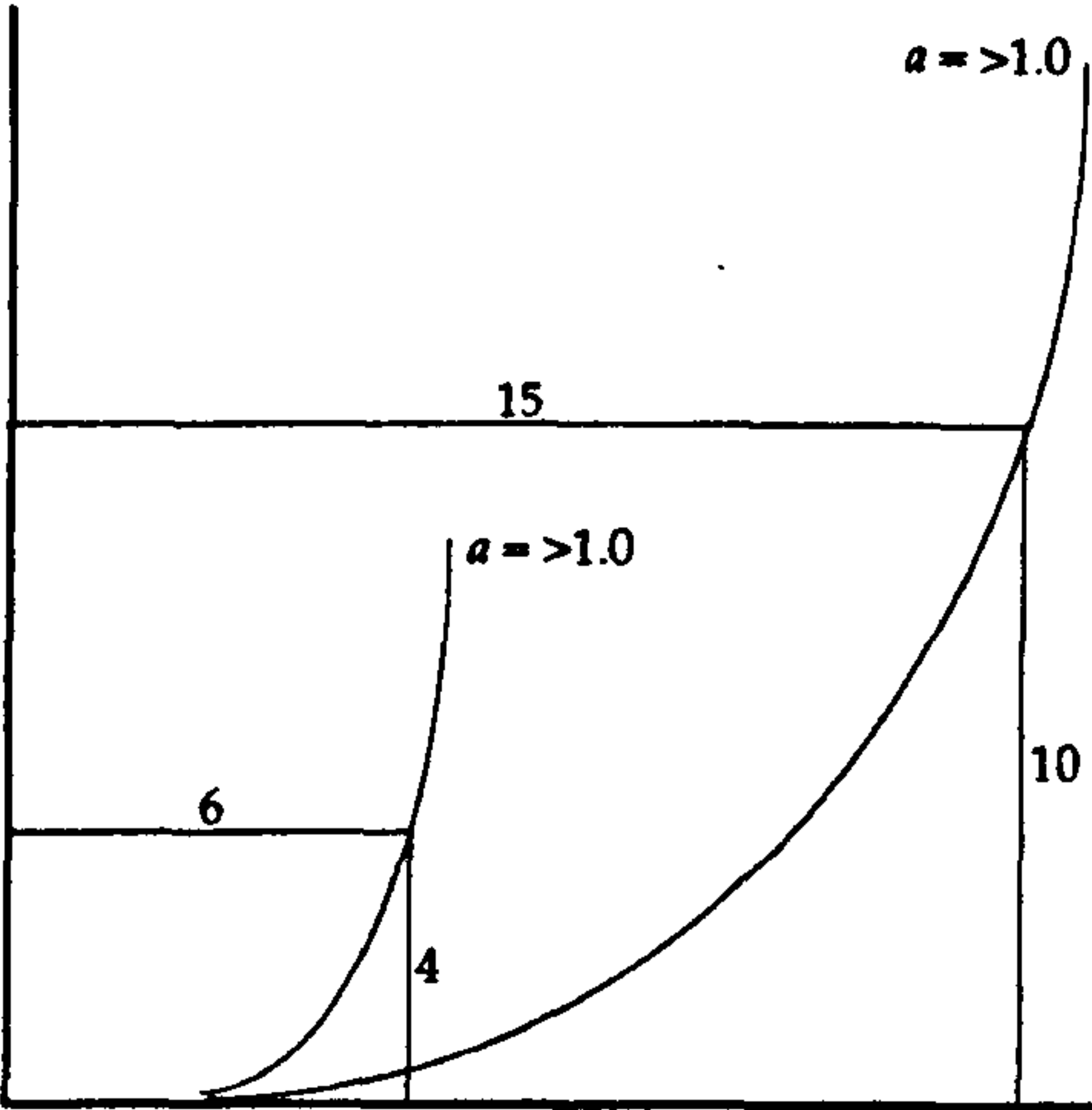


Figure 7.5. Allometric growth with 2 means on different growth curves, with the same ratios: $6/4 = 1.5$; $15/10 = 1.5$.

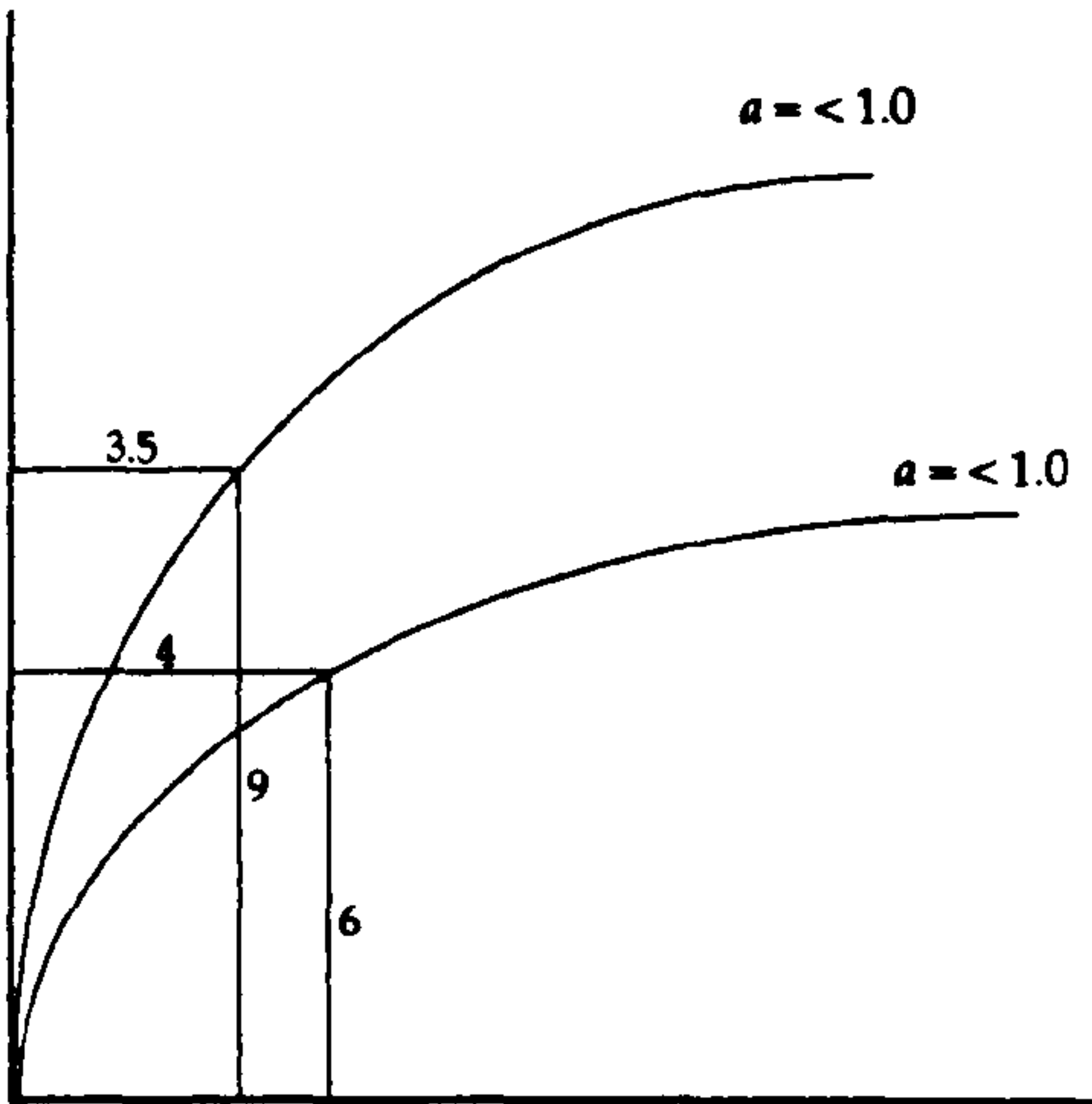


Figure 7.6. Allometric growth with 2 means on different growth curves, with different ratios: $3.5/9 = 0.39$, $4/6 = 0.67$.

7.1.2 Results of allometric testing on the 2 lineages used in this study

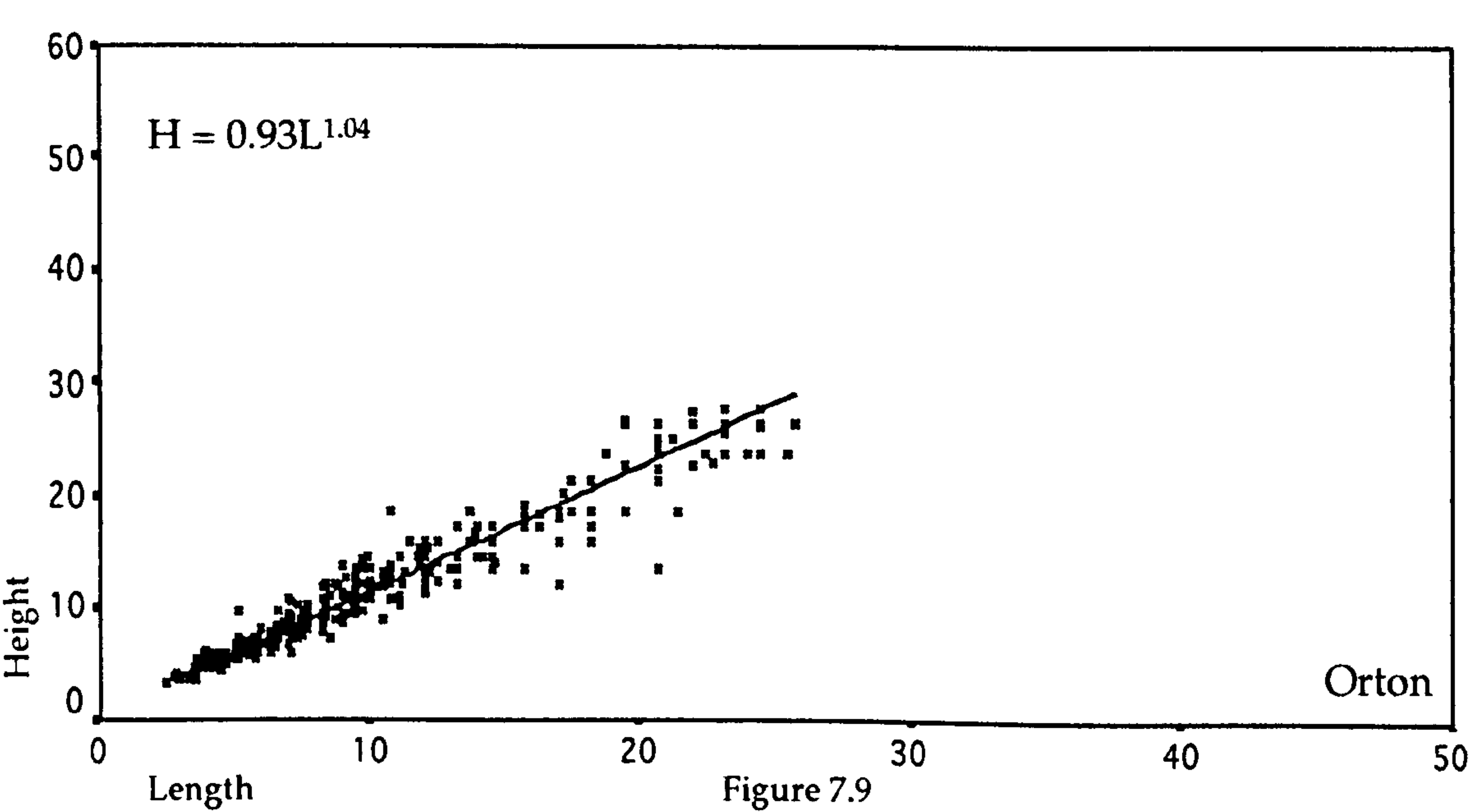
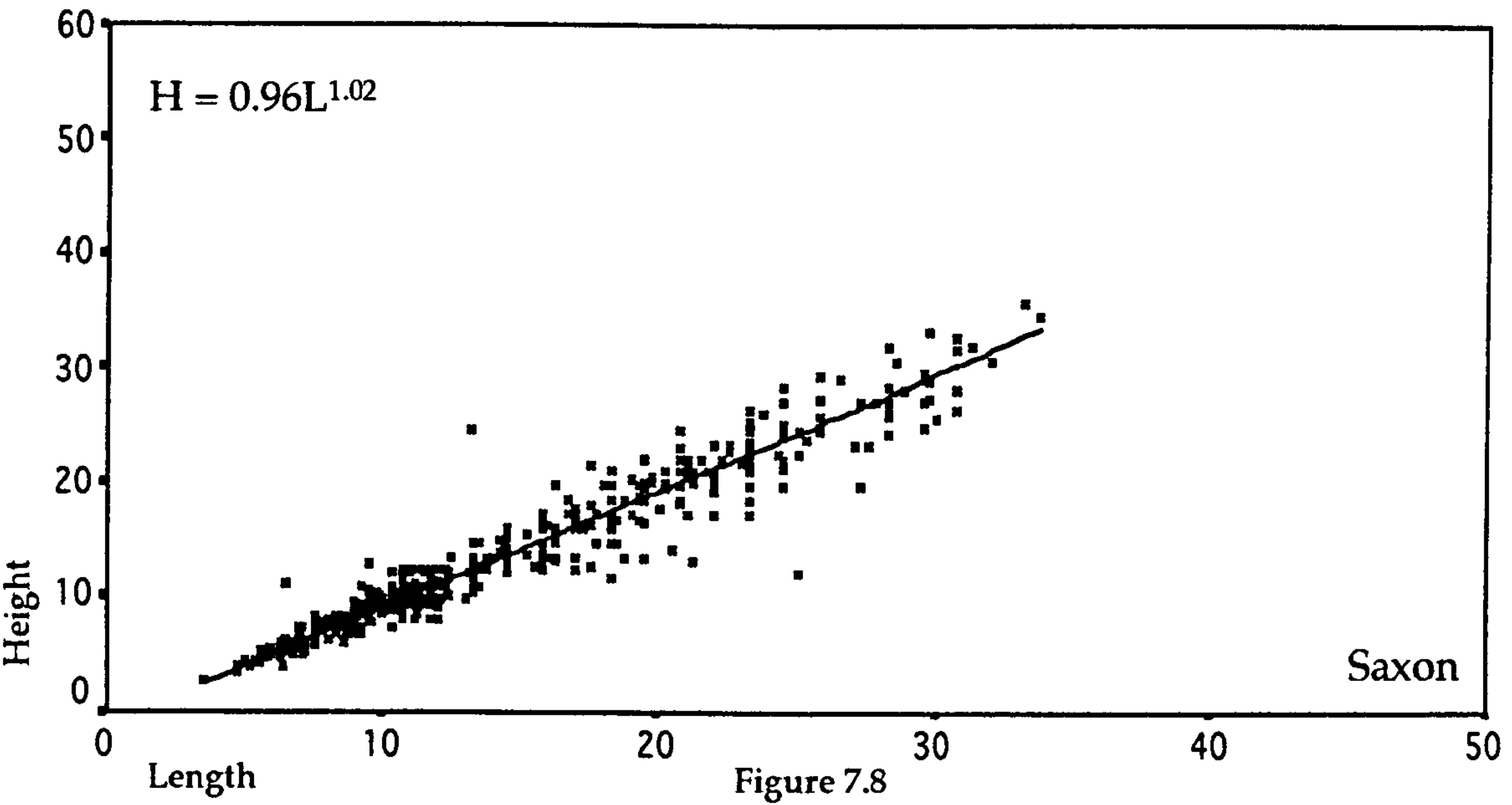
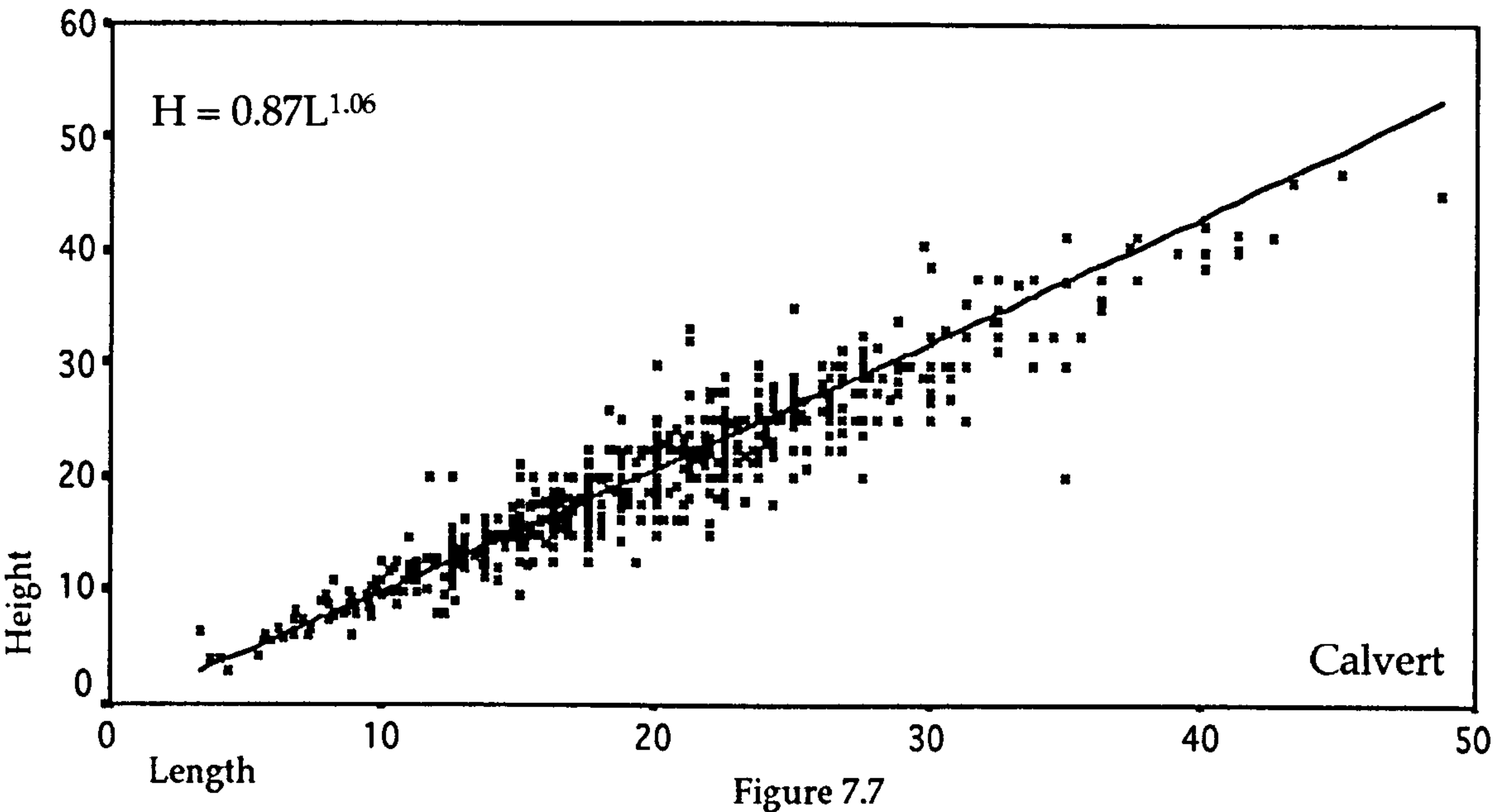
The procedure above (Section 7.1) was carried out on the four variates as two bivariate scatters: Length against Height and Hinge Length against Anterior Length, for each lineage at each pit; e.g. Length against Height for *M. braamburiensis* at Calvert pit etc., Figures 7.7-7.16. These show the relative growth for each total sample for each lineage and location:

Ratio, lineage and location	Figure number	<i>a</i>	<i>b</i>	<i>z</i>	<i>n</i>	Allometric (A) or Isometric (I) growth
L-H <i>M. braamburiensis</i> , Calvert pit	7.7	1.06	0.87	4.48	779	A
L-H <i>M. braamburiensis</i> Saxon pit	7.8	1.02	0.96	1.88	499	I
L-H <i>M. braamburiensis</i> Orton pit	7.9	1.04	0.93	2.74	384	A
L-H <i>M. morrisi</i> Calvert pit	7.10	0.89	0.79	-5.81	844	A
L-H <i>M. morrisi</i> Saxon pit	7.11	0.76	1.03	-12.58	920	A
HL-AL <i>M. braamburiensis</i> Calvert pit	7.12	0.94	0.93	-2.48	541	A
HL-AL <i>M. braamburiensis</i> Saxon pit	7.13	1.21	0.48	6.44	503	A
HL-AL <i>M. braamburiensis</i> Orton pit	7.14	1.20	0.44	6.83	358	A
HL-AL <i>M. morrisi</i> Calvert pit	7.15	0.55	1.49	-42.83	730	A
HL-AL <i>M. morrisi</i> Saxon pit	7.16	1.05	0.41	2.08	908	A

Table 7.1. Results of allometric testing for total sample at each location.

Figures 7.7-7.16 show the type of growth for the total sample for each ratio and lineage in each location. All ratios and lineages show allometric growth except the L-H ratio for *M. braamburiensis* at Saxon pit, which shows isometric growth. Note that all data is amalgamated for these plots, with samples of very different statistics being merged, hence the wide scatter of data around the best fit line.

This procedure illustrates only the overall type of growth for each ratio, lineage and location, it is not robust enough to determine how the growth might change through the section of Peterborough Member at each locality. All of the four possible growth scenarios illustrated in Figures 7.3-7.6 could occur through the section of Peterborough Member at the three locations.



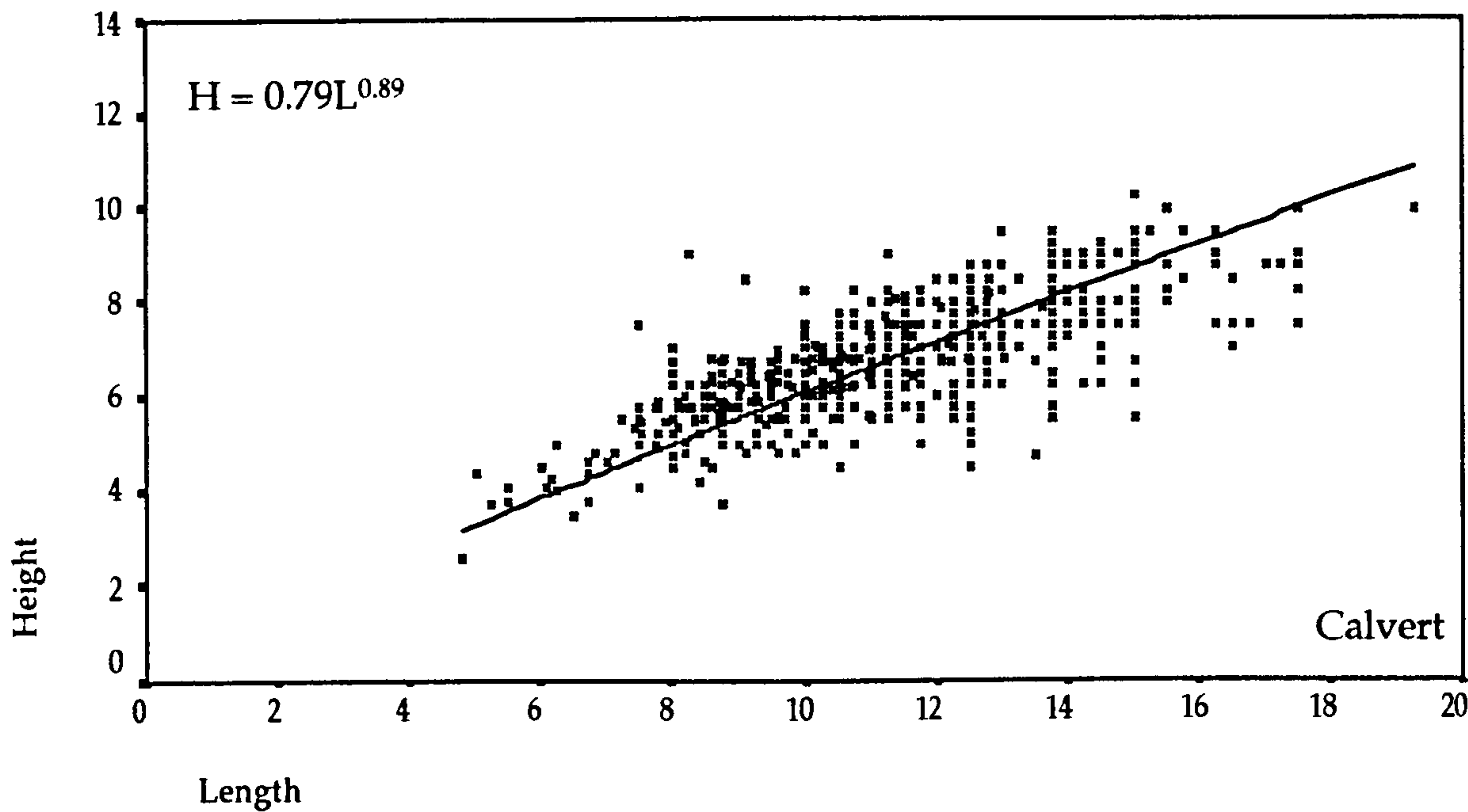


Figure 7.10

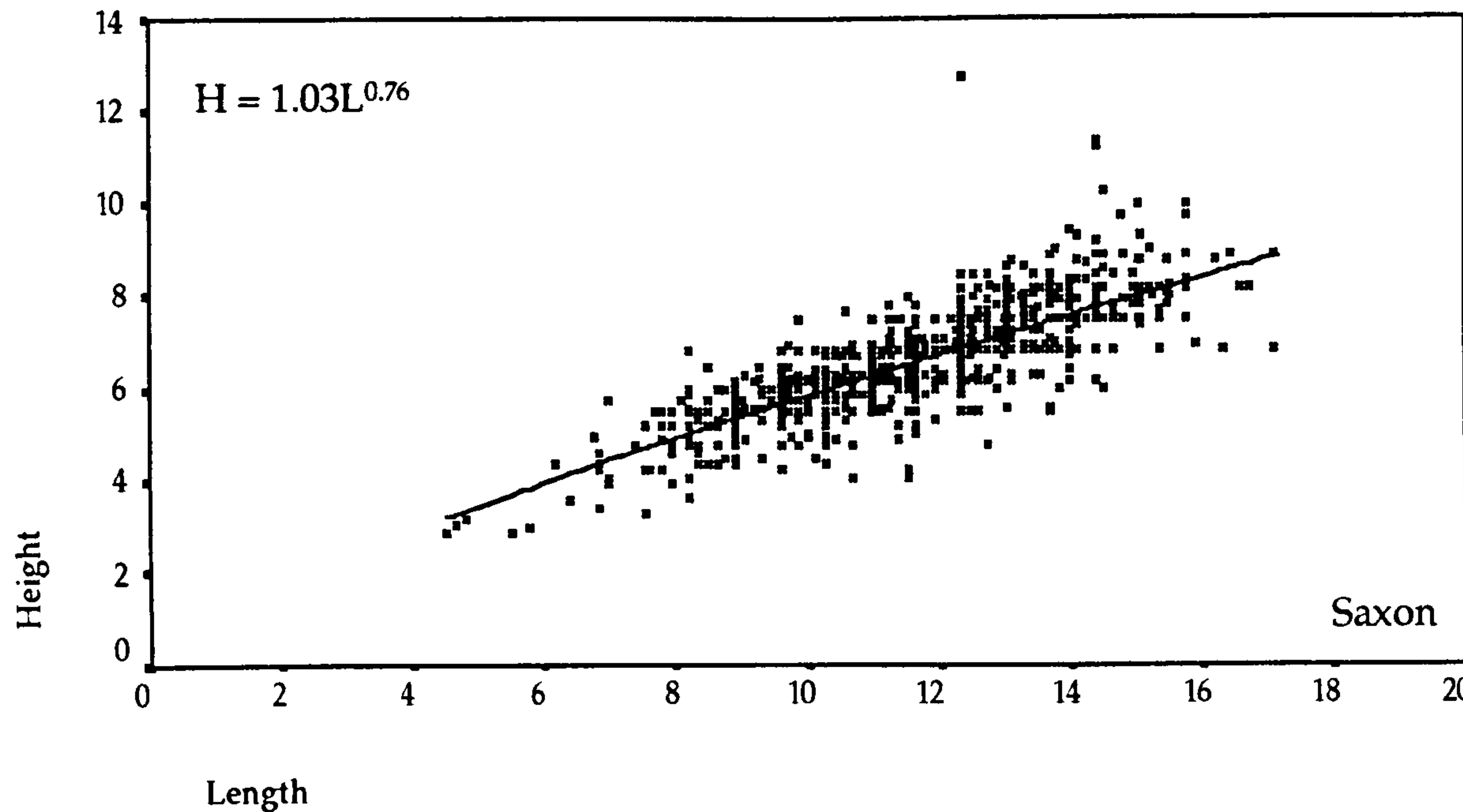
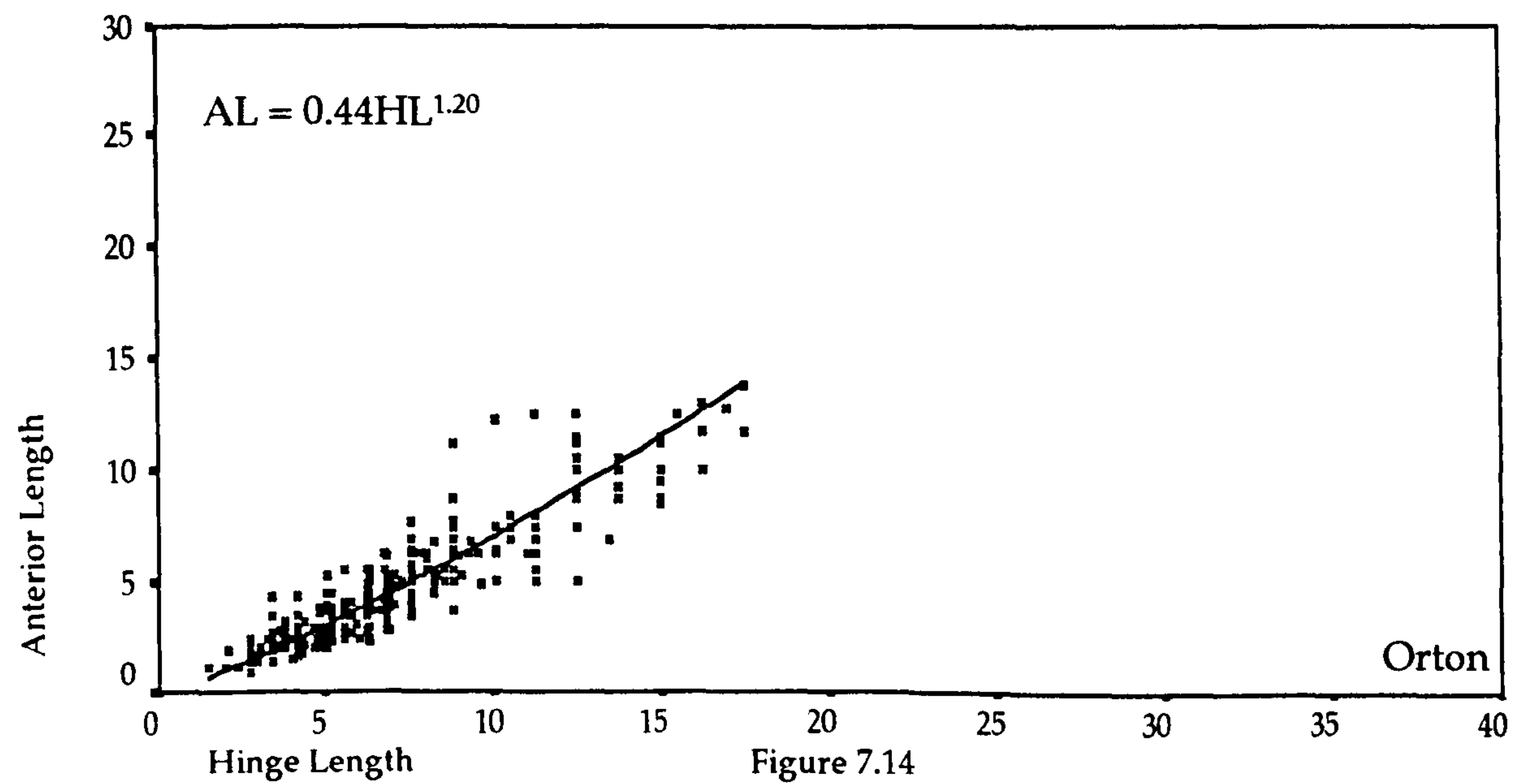
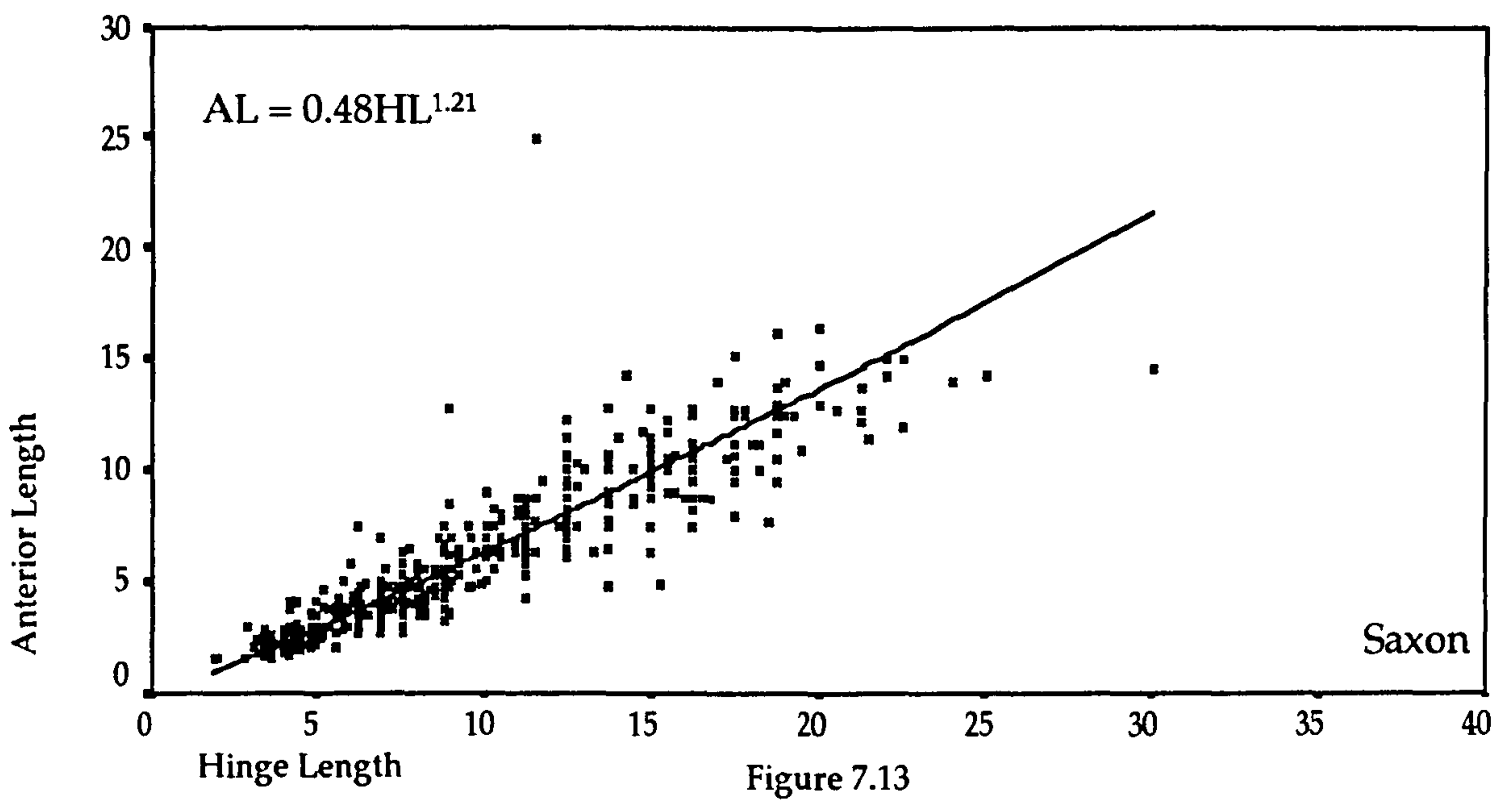
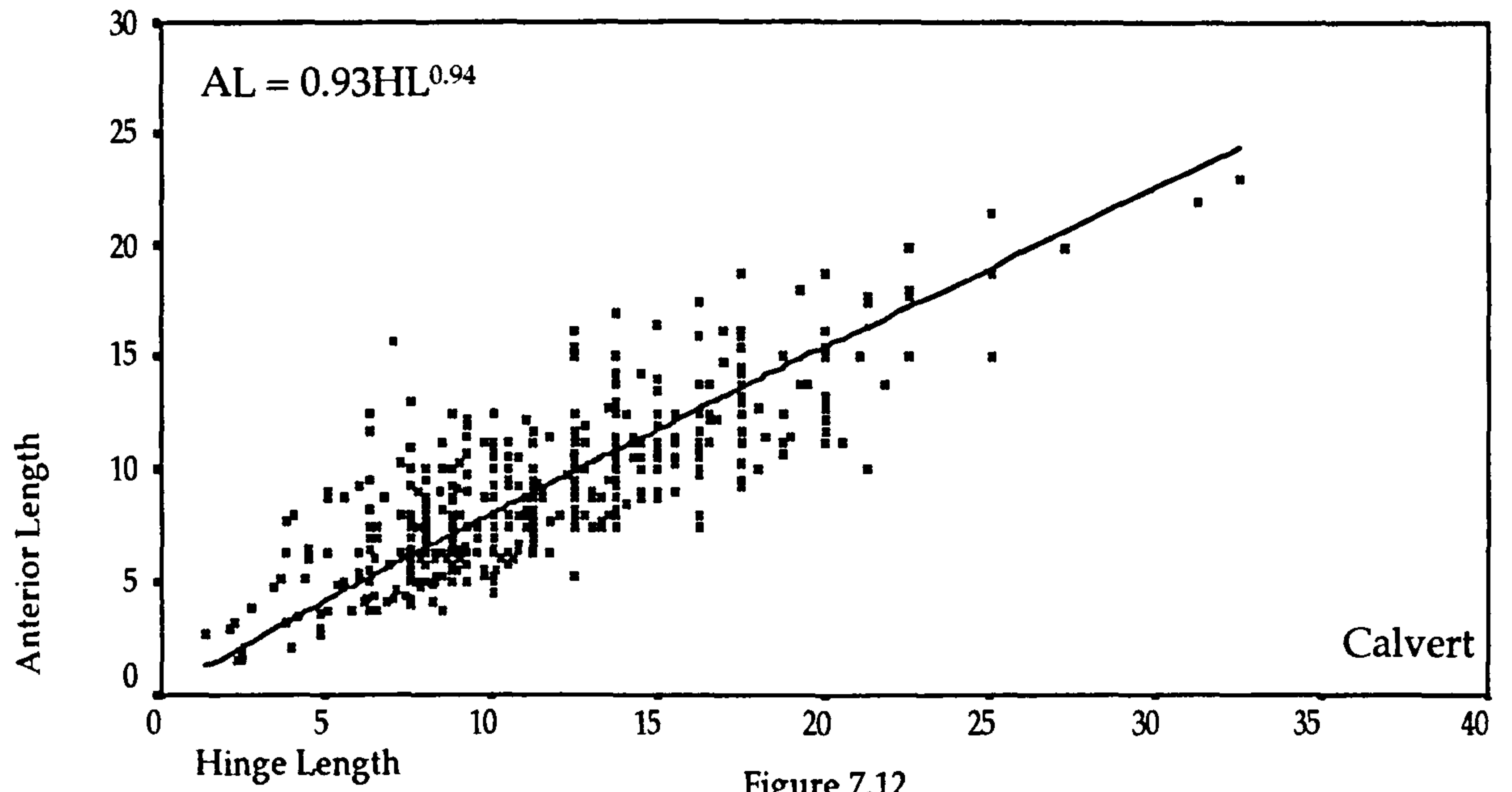


Figure 7.11



Growth curves for Hinge Length and Anterior Length,
M. morrisi, Calvert and Saxon pits.

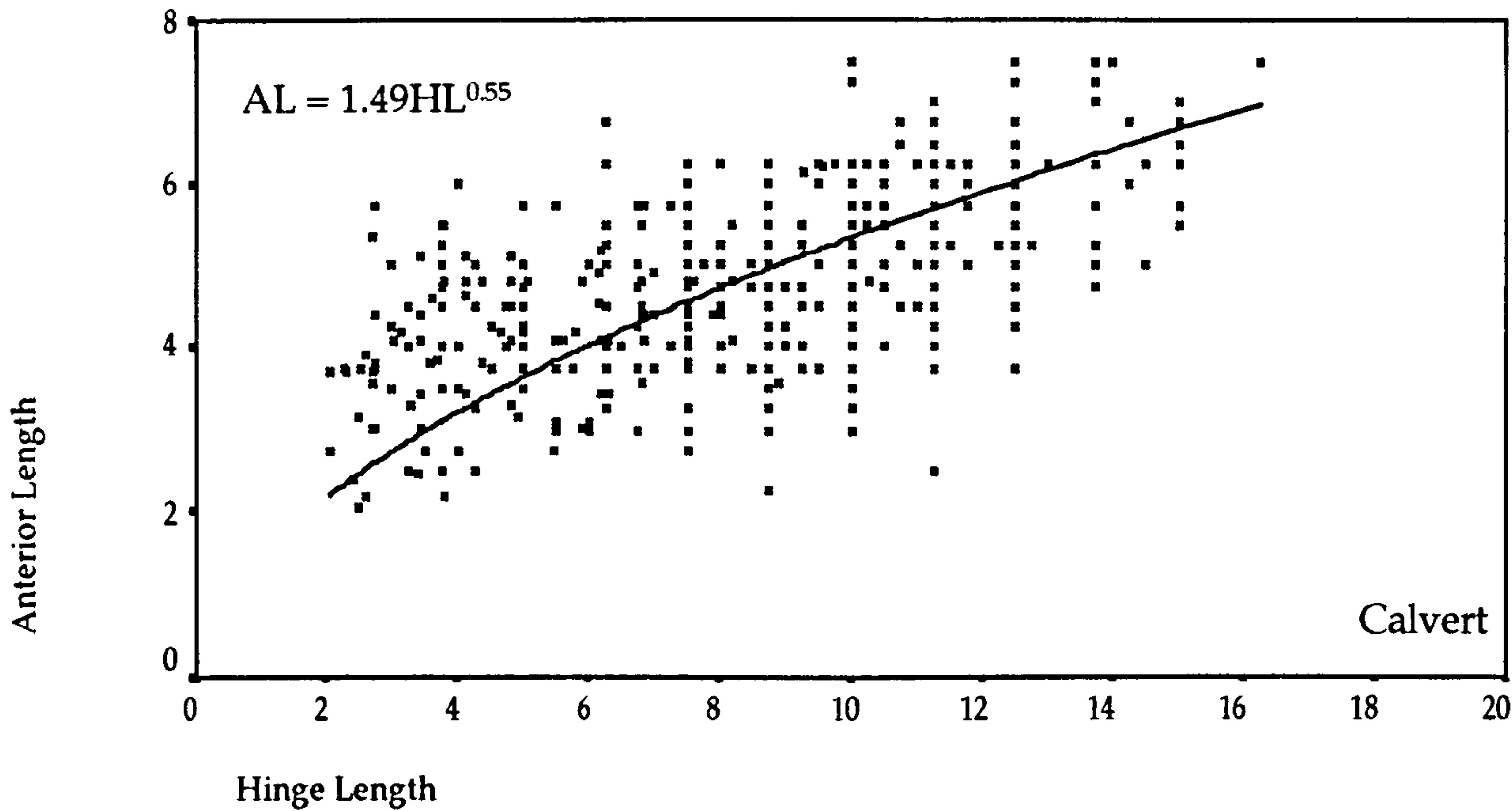


Figure 7.15

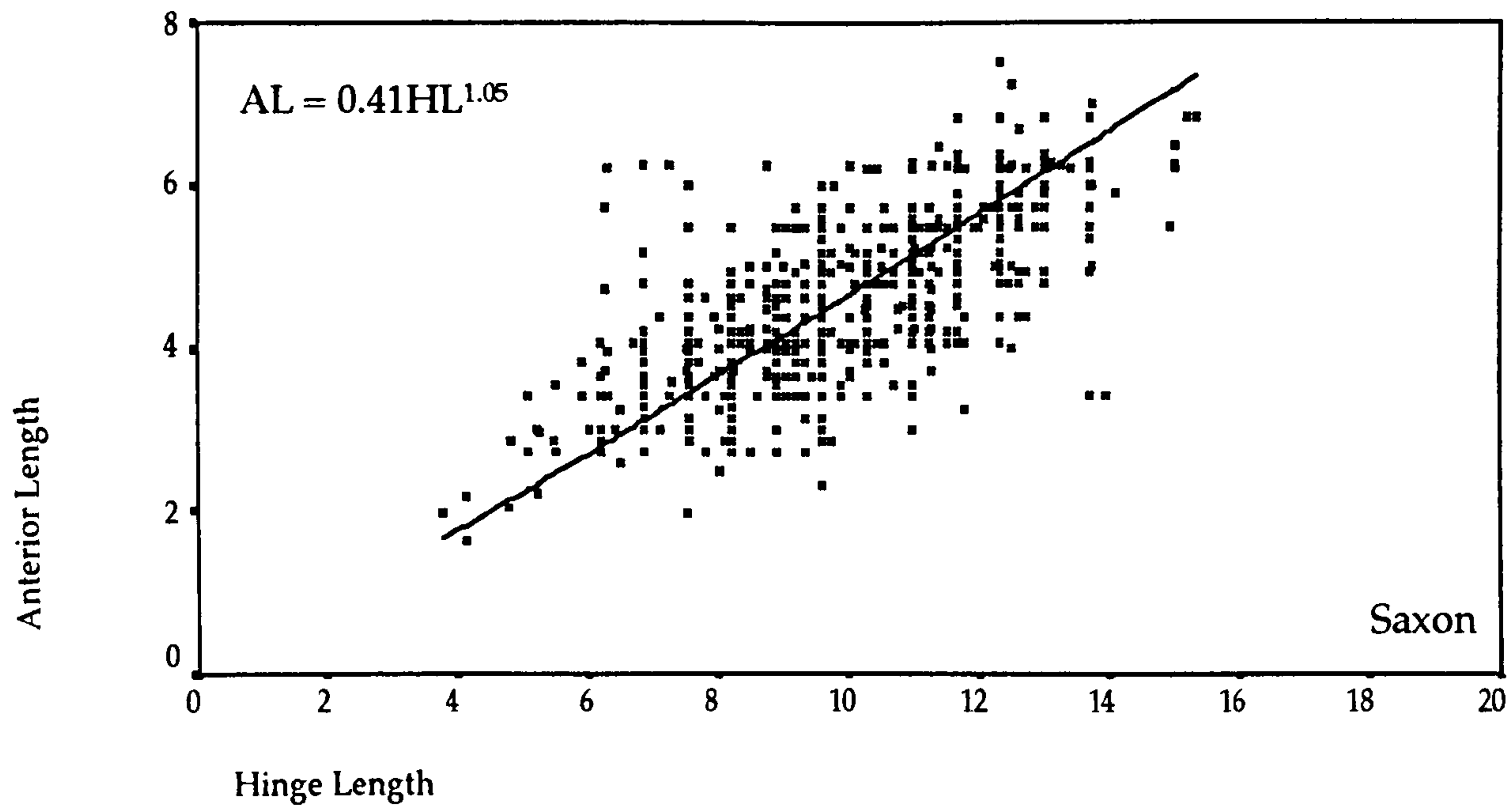


Figure 7.16

7.1.3 Detecting growth patterns for individual horizons

The growth patterns illustrated by Figures 7.7-7.16 are for the whole pits, but the growth patterns could vary considerably over the section. Thus the growth pattern of individual horizons was determined.

To obtain the growth patterns throughout the section, one must firstly calculate the a and Z values for each sample, according to equations 4 and 5. If growth between adjacent sample means is isometric then t-tests are used to compare the adjacent sample means to see if a significant change in ratio has occurred, i.e. morphological change. If adjacent sample means are allometric then one must compare them to see if a , the allometric exponent, has changed significantly or not, i.e. to see whether the adjacent samples lie on the same growth curve. The two adjacent sample means with allometric growth can be compared using the equation:

$$Z = a_1 - a_2 / s_p \quad (6).$$

where s_p is the pooled estimate of the standard deviations from both samples, n_1 and n_2 . The pooled standard deviation can be worked out using:

$$s_p = \sqrt{(n_1 - 1)\sigma_1^2 + (n_2 - 1)\sigma_2^2 / n_1 + n_2 - 2} \quad (7).$$

where σ_1 and σ_2 are the standard deviations for both samples.

Once the s_p has been calculated it can be placed into equation number (6) and z calculated. If z is greater or equal in magnitude to ± 1.96 then one can reject the null hypothesis 'that there is no difference between the a value of each sample', concluding that the a 's are significantly different to one another, and thus the samples belong to different growth curves. If this is the case then one can now conclude that there was a change in the pattern of growth, which is often interpreted as an evolutionary change, as patterns of relative growth commonly have a high degree of genetic determination (The Open University 1993)

Even if the a values from each sample are not considered significantly different, i.e. the slopes are not significantly different, the intercepts of the RMAs on the log y axis, i.e. the values of $\log b$ (hence b in the allometry equation, $y = bx^a$) can still differ, in which case the pattern of growth will have changed. Formal tests have been proposed for significant differences in the

intercepts $\log b$; however, statisticians are still unsure of their accuracy and so as yet these cannot be used.

7.1.4 Summary of Section 7.1

It is now possible to graph the bivariate scatter graphs as ratios on the horizontal axis against depth of sediment on the vertical axis. As previously stated, there are often problems with ratio graphs, as a change in ratio could just reflect sampling from a different part of the allometric growth curve. However, as all growth curves for individual horizons with a sample size of more than 27, for each ratio and lineage, have been calculated, it is possible to check if the samples came from populations with different growth curves. If adjacent sample means lie on isometric curves, then they can be compared using a t-test to see if they differ significantly or not (i.e. show significant shape change). If adjacent sample means both lie on allometric curves a significant difference in their a values suggests evolutionary change. Sample means with allometric growth adjacent to sample means with isometric growth have a different pattern of growth, and are therefore considered to show an evolutionary change as well.

7.2 Length to Height ratio for *M. braamburiensis*

Within this section the microevolutionary patterns of the Length to Height ratio for *M. braamburiensis* from the three locations, Calvert, Orton and Saxon pits, are discussed. Firstly a brief summary is given of the results from all three pits, then the results are considered in more detail from each individual pit in turn.

7.2.1 Explanation of symbols used on result graphs

Note, for the readers ease, Figures 7.17 to 7.89 are found within the separate book of figures. The data (Figures 7.18, 7.19, 7.20, 7.27, 7.28, 7.33, 7.34, 7.35, 7.42, and 7.43) are graphed by placing the variable on the x axis, against its position within the section on the y axis (in metres), with the base of the section at 0.0 m on the y axis. The section is then measured in metres up the y axis to the top of the section, for each locality. The x axis represents either the Length to Height ratio or the Hinge Length to Anterior Length ratio. The x axis

changes in scale depending on the ratio and lineage; however the scale remains identical for the same ratio in the same lineage, so that pits can be compared (e.g. the x axis for Length to Height ratio for *M. braamburiensis* will remain the same scale for all three pits).

The data are displayed as follows. The means are plotted for each horizon or sample (sampling interval), shown by a square. An error bar is superimposed across the mean to represent the range of the 95% confidence interval. The number at the end of this bar represents the number of individual specimens (sample size) that the mean and the confidence interval are based upon. The total number of individuals used for the entire graph is given in the top left hand corner. In the top right hand corner is a small line drawing of the lineage to which the data relate. An example is annotated in Figure 7.17.

All graphs are split into two sections: the More Stable Zone (MSZ) and the More Fluctuating Zone (MFZ). These are shown differently; on the y axis; the MSZ is represented by a wide solid black line, and the MFZ is represented by a dashed line. At Calvert pit the MSZ, from the studied section lies approximately between the base of the section, 0.0 m, and 4.8 m, with the MFZ lying approximately between 4.8 m and 12 m (the top of the section). At Saxon pit the MSZ lies approximately between the base of the section, 0.0 m, and 3.2 m, with the MFZ occurring approximately between 3.2 m and 12 m (the top of section). At Orton pit only the *obductum* Subzone of the Peterborough Member was studied due to removal of the upper subzones by glacial action. The *obductum* Subzone corresponds to the MSZ.

The data are displayed against stratigraphical position (in metres) within the dug section of each pit. However, it is often more useful to express individual sampling intervals as horizons (as defined in Section 5.3). Each horizon represents a 200 mm vertical interval of sediment; at each pit horizon numbers start from the base of section and number upwards, no matter where in stratigraphy the section starts. For comparison between horizon numbers and the stratigraphic height (in metres), the following conversion table should be used (or the bookmark provided):

Horizon Number	Stratigraphical height (M)	Horizon Number	Stratigraphical height (M)	Horizon Number	Stratigraphical height (M)	Horizon Number	Stratigraphical height (M)
1	20 cm	16	3.2 m	31	6.2 m	46	9.2 m
2	40 cm	17	3.4 m	32	6.4 m	47	9.4 m
3	60 cm	18	3.6 m	33	6.6 m	48	9.6 m
4	80 cm	19	3.8 m	34	6.8 m	49	9.8 m
5	1.0 m	20	4.0 m	35	7.0 m	50	10.0 m
6	1.2 m	21	4.2 m	36	7.2 m	51	10.2 m
7	1.4 m	22	4.4 m	37	7.4 m	52	10.4 m
8	1.6 m	23	4.6 m	38	7.6 m	53	10.6 m
9	1.8 m	24	4.8 m	39	7.8 m	54	10.8 m
10	2.0 m	25	5.0 m	40	8.0 m	55	11.0 m
11	2.2 m	26	5.2 m	41	8.2 m	56	11.2 m
12	2.4 m	27	5.4 m	42	8.4 m	57	11.4 m
13	2.6 m	28	5.6 m	43	8.6 m	58	11.6 m
14	2.8 m	29	5.8 m	44	8.8 m	59	11.8 m
15	3.0 m	30	6.0 m	45	9.0 m	60	12.0 m

Table 7.2. Relationship between metres and horizon number for the section of Peterborough Member sampled at each locality.

7.2.2 Overview of results

Location	Figure number	Initial mean ratio	Final mean ratio	Lowest mean ratio	Highest mean ratio	Overall average mean ratio for each pit
Calvert	7.18	0.96	0.97	0.88	1.04	0.99
Saxon	7.19	1.01	1.03	0.95	1.05	1.00
Orton	7.20	0.95	0.98	0.91	1.06	1.00

Table 7.3. Mean ratios for L-H ratio for *M. braamburiensis* at all three localities.

All three localities (Figures 7.18-7.20) have virtually equal overall mean ratios for this lineage and ratio. The initial mean ratio, final mean ratio, lowest mean ratio and highest mean ratio are also very similar between pits. At Calvert pit the initial mean and final mean ratio are also almost equal. The lowest and highest mean ratio deviate only slightly from these. Within the Saxon pit section the same pattern is also exhibited; the initial and final mean ratios are also very similar, the lowest and highest mean ratio deviate only slightly from these. At Orton pit the initial mean ratio is very similar to the final mean ratio, and again the lowest and highest mean ratios deviate only slightly from these.

7.2.3 Results after individual horizons were checked for allometric growth

Figures 7.21-7.23 and all other graphs of this nature for the other ratios and lineages have all been calculated using the methods described in Section 7.1 and 7.1.3. The symbols used are the same on each graph: samples are either coloured red or black. The red colour indicates that the sample has allometric growth. The black colour indicates that the sample has isometric growth (see Figure 7.17). Tables record the a and Z values for each sample.

By examination of Figures 7.21-7.23 it was noted, for both ratios that every adjacent sample either came from different populations (i.e. the test for significant differences in the a values when growth was allometric, found that the a values differed significantly, see Section 7.1.3), or were adjacent to isometric growth curves. Thus any significant shape changes detected were considered to be real shape changes. In general the symbols adopted for the figures are the same as those described within Section 7.2.1; however the red arrows between two samples illustrate significant differences between the two samples (see Figure 7.17).

7.2.3.1 Calvert pit

Figure 7.21 illustrates the results of allometric testing at Calvert pit, on horizons with $n > 27$ (Table 7.4). Within this ratio and lineage there were found to be only two significant differences between sample means with isometric growth (calculated using t-tests): the first between horizons 21 and 22, and the second between horizons 22 and 23 (4.2-4.4 m and 4.4-4.6 m). However, four horizons were found to be of allometric growth. Tests for significant differences in adjacent horizons found that they all changed significantly in the pattern of growth (see z values in Table 7.4).

Horizon number	<i>a</i> value	Z value	Sample size (n)	Allometric (A) / Isometric (I)	Test for significant difference in <i>a</i> (i.e. z value)
9	1.05	1.42	71	I	
10	1.22	1.88	28	I	
12	1.11	1.13	38	I	
13	1.20	2.34	34	A	-7.625
15	1.25	3.13	30	A	-3.63
17	1.14	2.08	37	A	7.259
18	1.18	2.49	40	A	-3.104
20	1.07	1.06	42	I	-72.36
21	1.08	1.38	47	I	
22	1.00		52	I	
23	1.06	1.17	39	I	
24	1.00		46	I	
40	1.00		30	I	
41	1.08	1.39	37	I	

Table 7.4. The type of growth for individual horizons, with n>27, for L-H ratio for *M. braamburiensis*, Calvert pit. (Z values are not given when the *a* value is 1.00, isometric growth, because the test for growth types did not need to be performed on these samples.) The test for significant difference in *a* values for allometric growth is given as the z value. The z value for the test between adjacent horizons is given against the higher horizon number, i.e. the z value for the test between horizons 12-13 is given against horizon 13.

7.2.3.2 Saxon pit

Figure 7.22 illustrates the result of allometric testing at Saxon pit, horizons with n>27 (Table 7.5). Unfortunately, this lineage at this pit was not as abundant and therefore there are fewer horizons with n>27 than at Calvert pit. All horizons tested are of isometric growth within this pit, therefore tests for significant differences in *a* values were not performed, only t-tests between adjacent horizons were undertaken. Only two significant differences (detected by t-tests) between adjacent horizons were found within this pit; between horizons 10-11 and 11-12 (2.0-2.2 m and 2.2-2.4 m).

Horizon number	<i>a</i> value	Z value	Sample size (n)	Allometric (A) / Isometric (I)	Test for significant difference in <i>a</i> (i.e. z value)
8	1.00		29	I	
10	1.00		36	I	
11	1.07	1.42	42	I	
12	1.00		37	I	
13	1.00		35	I	
14	1.05	1.8	63	I	

Table 7.5. The type of growth for individual horizons, with n>27, for L-H ratio for *M. braamburiensis*, Saxon pit. (Z values are not given when the *a* value is 1.00, isometric growth, because the test for growth type did not need to be performed on these samples).

7.2.3.3 Orton pit

Figure 7.23 illustrates the result of allometric testing, for Orton pit, on horizons with n>27 (Table 7.6). From the four horizons tested, three have isometric growth, and one horizon has allometric growth. Between the horizon with allometric growth (horizon 6) and the adjacent horizon (horizon 13) a significant change in the pattern of growth was recorded, see z values in Table 7.6. This was expected as the pattern of growth changes from isometric to allometric There were found to be no significant differences between horizons (detected by t-tests) for this lineage and ratio at Orton pit.

Horizon number	<i>a</i> value	Z value	Sample size (n)	Allometric (A) / Isometric (I)	Test for significant difference in <i>a</i> (i.e. z value)
6	1.12	2.92	64	A	
13	1.00		46	I	12.049
14	1.00		29	I	
16	1.00		44	I	

Table 7.6. The type of growth for individual horizons, with n>27, for L-H ratio for *M. braamburiensis*, Orton pit. (Z values are not given when the *a* value is 1.00, isometric growth, because the test for growth type did not need to be performed on these samples). The test for significant difference in *a* values for allometric growth is given as the z value. The z value for the test between adjacent horizons is given against the higher horizon number, i.e. the z value for the test between horizons 6-13 is given against horizon 13.

7.2.4 Interpretation of patterns from the Length to Height ratio for *M. braamburiensis*

This section interprets the results of Figures 7.18-7.26. Figures 7.24-7.26 show growth curves for each ratio and lineage at each locality. All growth curves are drawn, according to the equation $y=bx^a$, with the two variates (in millimetres) on the x and y axis. All growth curves are only drawn over the range of data points. The growth curves have different colours depending on the horizon they represent (this is so that their place in the stratigraphy can be identified easily):

blue curves = horizons 1-10;

red curves = horizons 11-20;

black curves = horizons 21-30;

green curves = horizons 31-40;

pink curves = horizons 41-60.

The black square on each growth curve represents the mean value for the variates at that horizon. The number at the end of the curve is the horizon number and *not* the sample size.

(Note some examples of individual patterns of relative growth i.e. for individual horizons, with all data points are shown in Appendix 6.)

7.2.4.1 Calvert pit

Figures 7.18 and Figure 7.21 illustrate the data for Length to Height ratio for *M. braamburiensis* at Calvert pit, with Figure 7.21 showing only sample means with $n \geq 27$. Previously (Section 7.2.2) this lineage was described as having virtually identical mean ratios at the beginning and end of the section.

Figure 7.21 shows mainly isometric growth (black squares) with some allometric growth (red squares) throughout the section. Where adjacent sample means both lie on allometric growth curves or on isometric and allometric growth curves comparisons between ' a ' were made. It was found that each adjacent allometric growth curve had significantly different ' a ' values. This indicates that there are changes in the pattern of growth between these adjacent horizons (12-13, 13-15, 15-17, 17-18 and 18-20), at least in the relationship between Height and Length. The interpretation therefore, is that it is highly plausible there are evolutionary changes between these horizons, because, they occur within the MSZ, therefore environmental fluctuations

could not have affected the data, and patterns of relative growth commonly have a high degree of genetic determination (see Section 7.10 for discussion of ecophenotypic verses genotypic variation). T-tests were performed between adjacent horizons to check for a significant difference in ratio, and therefore shape change. There were only two places within the section where the t-test highlighted any significant changes in ratios. These two significant changes between horizons 21-22 and 22-23 occurred within the MSZ. All of the significant morphological changes either by a change in growth or a change in ratio were found within the MSZ, with no significant morphological changes occurring within the MFZ, however it should be noted that there is a lack of data within the MFZ compared with data in the MSZ.

The growth curves for the horizons denoted in Table 7.4 are shown in Figure 7.24, with the mean for each variate on the curve (see also Table A2.1; any table number with A2 in front denotes a table in Appendix 2). From visual examination one can see that the majority of means are all clustered together around 20 mm Height and 20 mm Length. Overall, the growth curves plot extremely close together, and although each horizon has its own curve, the fact that they are so tightly constrained and the means from all horizons are clustered suggests that no additional significant differences in morphology between samples can be detected to those detected by the t-tests. Table A2.1 indicates no more growth pattern changes than those previously reported in Table 7.4.

The data were previously interpreted (Section 7.2.2) as having little deviation from the overall mean ratio as the beginning and end mean ratios are virtually identical, giving an overall pattern of net stasis. However, numerous morphological changes have been found within the MSZ.

T-tests were used over a larger range of data to check the assumption that the pattern of net stasis was correct. T-tests were carried out:

- (1) from the base of the section to the top of the section;
- (2) from the base of the section to the top of the MSZ;
- (3) from the start of the MFZ to the top of the section

The null hypothesis here is 'there is no difference between the samples being tested.' These results are recorded in Table 7.7.

The t-test performed on the data from the base to the top of the section show that there is no difference in means, thus suggesting that there is no significant morphological change over the whole section. The t-test performed on the data from the base of the section to the top of the MSZ shows that there is no difference in means here either, again suggesting little significant morphological changes over that zone, and that is the same for start of the MFZ to the top of the section. Thus, although there are significant morphological changes and growth pattern changes within the MSZ, they do not form a net directional change, and therefore an impression of overall net stasis is given for the Length to Height ratio for *M. braamburiensis*, Calvert pit.

	<i>M. braamburiensis</i>		<i>M. morrisi</i>	
	L-H	HL-AL	L-H	HL-AL
Calvert Pit				
Base to top	.801	.001	.000	.000
Base to top MSZ	.503	.000	.000	.000
Start MFZ to top	.732	.482	.000	.000
Saxon Pit				
Base to top	.716	.576	.113	.010
Base to top MSZ	.663	.066	.014	.407
Start MFZ to top	.959	.132	.787	.014
Orton Pit				
Base to top	.575	.524	X	X
Base to top MSZ	.575	.524	X	X
Start MFZ to top	X	X	X	X

Table 7.7. Results of t-Tests for all three localities, for both ratios and both lineages (X = no data). Results show whether significant differences occur between the base of the section and top of the section, between the base of the section and the end of the MSZ; and from the end of MSZ to the top of each section, at the 95% confidence level.

7.2.4.2 Saxon pit

Figures 7.19 and 7.22 illustrate the Length to Height ratio for *M. braamburiensis*, at Saxon pit. Previously (Section 7.2.2) Figure 7.19 was described as having virtually the same mean ratio at the beginning and end of the section, with only slight deviation around the overall mean ratio. This suggests a pattern of net stasis for this ratio and lineage, the same as observed in the Calvert section. Figure 7.22 illustrates two significant differences between adjacent samples, these show significant morphological changes within this species during the MSZ. There were no data from the MFZ (as

shown in Figure 7.22), due to numbers of individual specimens declining in this zone.

Growth curves were also plotted for all horizons in Table 7.5. However, because there were no horizons with a population $n > 27$ within the MFZ, all growth curves for horizons with $n > 14$ were plotted as well, which allowed growth over the whole section to be observed, see Figure 7.25 (Table A2.2). All growth curves are bunched together, with the majority of means clustered around 15 mm Height and 15 mm Length. A smaller group of means clusters around 22 mm Height and 23 mm Length; these horizons are within the MFZ. However, the tight bunching of the growth curves and the fact that the growth curves for the horizons within the MFZ (black and green) are mixed with the growth curves from the lower horizons (red and blue) suggests there has been little significant shape change over the section, and that the Length and Height have remained in net stasis. In Table A2.2 there are some growth shape changes, at least in the relationship between Length and Height, between adjacent horizons with $n > 14$ 15-27, 27-28, 28-29, 29-30 and 30-33. (Horizons 27, 29 and 30 are of allometric growth and lie adjacent to horizons with isometric growth). These growth shape changes, however, are confined to just one area in the section.

T-tests were performed on the data (Table 7.7) from the base to the top of the section; base of the section to the top of the MSZ; and from the start of the MFZ to the top of the section. No significant differences were found suggesting that the pattern is one of net stasis. Therefore overall the H-L data for *M. braamburiensis* from Saxon pit shows a pattern of overall net stasis, with some changes, but not in any one direction, in the pattern of growth within the MFZ.

7.2.4.3 Orton pit

Figures 7.20 and 7.23 illustrate the Length to Height ratio for *M. braamburiensis*, at Orton pit. Previously (Section 7.2.2) it was suggested that the beginning and end means of this section were virtually equal, with slight variations of the means about the overall mean ratio. Figure 7.23 shows that there were no significant morphological changes found, from t-tests, within the MSZ for this lineage and ratio at Orton pit. A growth pattern change between horizons 6-13 was observed, which is within the MSZ.

On closer examination of Figure 7.20 there appears to be a trend within part of these data. Between the base of the pit and horizon 6 (1.2 m) the mean apparently shifts towards a higher value. The t-test result (comparing the base mean ratio, horizon 1 with horizon 6) of $P = 0.687$, shows however, that there was no significant difference in the samples, although there is only a very little overlap between the error bars. A slightly larger sample size may have revealed net change.

Figure 7.26 shows the growth curves for horizons with samples of $n > 12$ (Table A2.3). The growth curves during this MSZ do not change dramatically in the pattern of growth; all curves appear to be bunched at their bases, with the tops diverging slightly. Although the means are not clustered together, they do not systematically change with increasing horizon number, suggesting little systematic morphological change as suggested above. Table A2.3 indicates changes in the pattern of growth, at least in the relationship between Length and Height, between horizons, with $n > 12$: 4-6, 6-8, 9-10 and 10-13.

The t-test data, Table 7.7, shows that from the base of the section to the top of the section/end of the MSZ, there is no significant difference in samples thus suggesting no significant morphological change over the section. This is the only t-test that can be performed for this section as the MFZ is not represented.

Therefore, for Length to Height ratio for *M. braamburiensis* at Orton pit, the overall pattern is of net stasis, with some deviation of growth pattern, which could be said to be evolutionary, but not in any one direction.

7.3 Length to Height ratio for *M. morrisi*

Within this section the microevolutionary patterns of the Length to Height ratio for *M. morrisi* from Calvert and Saxon pits are discussed. There are no data from Orton pit for this lineage. Firstly a brief summary is given of the results from both pits, then the results are considered in more detail from each individual pit in turn.

7.3.1 Overview of the results

Location	Figure number	Initial mean ratio	Final mean ratio	Lowest mean ratio	Highest mean ratio	Overall average mean ratio for each pit
Calvert	7.27	1.52	1.92	1.50	1.92	1.68
Saxon	7.28	1.56	1.76	1.48	1.84	1.76
Orton	X	X	X	X	X	X

Table 7.8. Mean ratios for L-H ratio for *M. morrisi* at Calvert and Saxon pits.

Both Calvert and Saxon pits (Figures 7.27 and 7.28) have similar initial mean ratios and lowest mean ratios. The final mean ratios, however are quite different, and the highest mean ratio also differs. This is reflected in the differing overall average mean ratio of the two pits. At Calvert pit the initial mean ratio is very different to the final mean ratio, but with little deviation outside these two. At Saxon pit there are also differences between the initial mean ratio and final mean ratio, but not to such a large extent as observed at Calvert pit. There is also slightly more deviation of the lowest and highest mean ratio around these two than seen at Calvert pit. This is the same ratio as examined in Section 7.2 but in a different lineage.

7.3.2 Results after individual horizons were checked for allometric growth

7.3.2.1 Calvert pit

Figure 7.29 illustrates the result of allometric testing for horizons with $n > 27$ (Table 7.9), for Calvert pit. All horizons except one show isometric growth. The test of difference in a 's between that one horizon (horizon 4) and horizon 5 (isometric growth) shows there to be significant change in the pattern of growth (see z value in Table 7.9). This was expected as there is a difference in growth pattern between allometric and isometric growth curves. There were four significant differences found between adjacent sample means with isometric growth, using t-tests: between horizons 11-13 (2.2-2.8 m), 13-24 (2.6-4.8 m), 33-38 (6.6-7.6 m), and 38-50 (7.6-10 m).

Horizon number	<i>a</i> value	Z value	Sample size (n)	Allometric (A) / Isometric (I)	Test for significant difference in <i>a</i> (i.e. z value)
4	0.75	-3.68	46	A	-24.25
5	1.00		35	I	
11	0.88	-1.25	28	I	
13	1.20	1.34	29	I	
24	1.00		28	I	
25	1.00		42	I	
26	1.17	1.58	59	I	
27	0.87	-1.05	41	I	
28	1.17	1.23	41	I	
29	0.87	-1.67	48	I	
30	1.00		39	I	
32	1.20	1.38	35	I	
33	1.00		28	I	
38	1.00		45	I	
50	1.14	1.08	44	I	

Table 7.9. The type of growth for individual horizons, with n>27, for L-H ratio for *M. morrisi*, Calvert pit. (Z values are not given when the *a* value is 1.00, isometric growth, because the test for growth type did not need to be performed on these samples.) The test for significant difference in *a* values for allometric growth is given as the z value. The z value for the test between adjacent horizons is given against the higher horizon number, i.e. the z value for the test between horizons 4-5 is given against horizon 5.

7.3.2.2 Saxon pit

Figure 7.30 illustrates the result of allometric testing on horizons with n>27 (Table 7.10), for Saxon pit. All horizons tested were found to be of isometric type growth. There were only two places where significant differences were found using t-tests; horizons 41-42 (8.2-8.4 m) and 45-47 (9.0-9.4 m).

Horizon number	<i>a</i> value	Z value	Sample size (n)	Allometric (A) / Isometric (I)	Test for significant difference in <i>a</i> (i.e. z value)
16	1.00		39	I	
22	1.17	1.19	34	I	
23	1.00		42	I	
24	1.00		51	I	
26	1.00		49	I	
34	1.00		34	I	
35	1.43	1.86	52	I	
38	1.17	1.71	60	I	
39	1.00		57	I	
41	0.90	-1.64	37	I	
42	0.89	-1.64	33	I	
45	0.86	-1.60	30	I	
47	1.00		34	I	
49	1.00		28	I	

Table 7.10. The type of growth for individual horizons, with $n > 27$, for L-H ratio for *M. morrisi*, Saxon pit. (Z values are not given when the *a* value is 1.00, isometric growth, because the test for growth type did not need to be performed on these samples.)

7.3.3 Interpretations of patterns from the Length to Height ratio for *M. morrisi*

This section interprets the results of Figures 7.27-7.32. Figures 7.31 and 7.32 are the growth curves for Calvert and Saxon pits.

7.3.3.1 Calvert pit

Figures 7.27 and 7.29 illustrate the Length to Height ratio for *M. morrisi* at Calvert pit. Previously (Section 7.3.1) Figure 7.27 was shown to have a large positive difference between the means at the beginning and end of the section. Figure 7.29 shows four significant changes in adjacent sample means with isometric growth (red arrow); two significant morphological changes occur between adjacent samples in each of the MSZ and the MFZ. There was also a significant change in the pattern of growth between horizons 4 and 5 within the MSZ.

The overall pattern observed within this data (Figure 7.27) is clearly one of positive net morphological change (+NMC). The +NMC occurs between the base of the pit and the end of the MSZ. At the change-over point between the MSZ and MFZ, the observed trend of the data suddenly changes, to net stasis. Net stasis continues for one metre from 4.8 m to 5.8 m. This pattern appears to tally with the plus ça change model because at the point of change between the

MSZ and the MFZ the environment appears to have been in its most fluctuating state, before returning to a calmer environment further into the MFZ (after 5.8 m, during beds JC10A, JC10C and JC10D, see Section 6.3.2). As the environmental variables become calmer the data trends in a more positive net morphological change once more.

Figure 7.31 shows the growth curves for horizons with a population of $n > 24$ (Table A2.4). Looking at the colour scheme for the growth curves, one can see that on the left hand side of the graph is a blue curve, followed by red curves, then black and green curves together, and finally pink curves. The growth curves progress from left to right at approximately the same angle, suggesting that the Length has grown at a faster rate than the Height. The means (black squares) show an increase in Length greater than Height. The plotted growth curves and their means reinforce the conclusions made above, that there is more shape change in the MSZ (blue and red curves) and then less shape change within the MFZ (black, green and pink curves). However, these changes in the pattern of growth are not reflected in differences in a . Table A2.4 indicates no more changes in the pattern of growth than previously shown in Table 7.9. Therefore the visual changes in growth pattern seen on Figure 7.31 are thought to represent changes in the b values which cannot be statistically tested.

However, Figure A5.1 (Appendix 5) illustrates a plot of 'a' and 'b' values. The plot shows distinctly a pattern of opposites; that is as 'a' increases 'b' decreases and vice versa. What is apparent from this plot is that the overall pattern is of gross stasis. This is not the same as the pattern produced from the Length to Height ratio on Figure 7.29, which is for considerable change both in the MSZ and MFZ, with a period of stasis at the beginning of the MFZ. During this period of stasis (4.8-5.8 m; observed on Figure 7.29), the 'a' and 'b' values appear to fluctuate quite dramatically on Figure A5.1. However, the greater amplitude of 'a' and 'b' actually occur within the MSZ. There is a hint of a shift in the 'a' and 'b' values after 5.8 m where the 'a' value increases and the 'b' value decreases, see Figure A5.1. These patterns appears to match with the pattern of change in Figure 7.29, however, the whole plot (see Figure A5.1) appears like a lot of background noise in a pattern of overall net stasis.

T-tests show (Table 7.7) from the base to the top of the section a significant difference between the samples. Samples from the base of the section to the end of the MSZ were also found to be significantly different, and this trend was also observed from the start of the MFZ to the top of the section. Therefore, according to the t-tests, each of the two zones showed +NMC. However, these data does show some net stasis at the beginning of the MFZ; a t-test was run over this part of the section (4.8 m - 5.8 m), and the results ($P=0.936$) showed that there was no significant difference in samples.

Overall for this lineage and ratio at Calvert pit, the morphological pattern is one of +NMC with morphological variation in sample means both within the MSZ and the MFZ, with a period of net stasis during the most fluctuating part of the section (4.8-5.8 m).

7.3.3.2 Saxon pit

Figures 7.28 and 7.30 illustrate the Length to Height ratio for *M. morrisi* at Saxon pit. Previously (Section 7.3.1), Figure 7.28 was described as having different beginning and end mean ratios, with some deviation from the overall mean ratio, and deviation outside boundaries of the beginning and end mean ratios fairly often. For all horizons tested in Figure 7.30, all were considered to be isometric in growth; therefore any significant differences in the samples could be considered as being true shape changes. Two significant differences between adjacent mean ratios were found, both being in the MFZ. None were found in the MSZ, but sample size here was much lower, making it less likely to find significant differences.

- Figure 7.32 shows the growth curves for horizons of populations $n>24$ (see Table A2.5). All growth curves are bunched together from across the whole studied section, with pink curves (horizons 41-60) somewhat overlapping with blue curves (horizons 1-10). There is clustering of means around 6.5 mm Height and 12 mm Length. The ' a ' values in Table A2.5 indicate there are some changes in the pattern of growth, at least in the relationship between Length and Height, when horizons with $n>24$ are compared; between horizons 2-16, 26-27 and 27-32. Allometric growth was expected for horizon 2, as the curve on Figure 7.32 is clearly not linear, this was confirmed by the tests. Whereas the growth curves themselves show little overall evolutionary change.

However, t-test data (Table 7.7) indicates a significant morphological change between the start of the section and the top of the MSZ, whereas t-test data indicates no changes in morphology over the MFZ; thus suggesting net stasis during this zone. Figure 7.28 shows that during the MSZ there is an overall positive shift in samples, from a ratio of 1.56 to a ratio of 1.77, whereas 1.76 is the final ratio. Hence over the MFZ there is virtually no change in mean ratio from the start of the MFZ to the end of the MFZ; the t-test data confirms this.

Figure 7.28 shows +NMC over the MSZ with numerous positive and negative shifts in means. During the MFZ, the negative (or reversal) shifts cancel out the positive shifts, giving an overall impression of net stasis.

7.4 Hinge Length to Anterior Length for *M. braamburiensis*

Within this section the microevolutionary patterns of the Hinge Length to Anterior Length ratio for *M. braamburiensis* from Calvert, Saxon and Orton pits are discussed. Firstly a brief summary is given of the results from all three pits, then the results are considered in more detail from each individual pit in turn.

7.4.1 Overview of results

Location	Figure number	Initial mean ratio	Final mean ratio	Lowest mean ratio	Highest mean ratio	Overall average mean ratio for each pit
Calvert	7.33	0.79	1.50	0.65	1.50	1.29
Saxon	7.34	1.77	1.21	1.21	1.78	1.65
Orton	7.35	1.42	1.41	1.41	1.80	1.59

Table 7.11. Mean ratios for HL-AL ratio for *M. braamburiensis* at all three localities.

Figures 7.33-7.35 illustrate this ratio in this lineage for all three pits. Unlike the L-H ratio for *M. braamburiensis*, there are differences between the means obtained in all three localities. The means given in Table 7.11 show a lower overall average mean ratio in Calvert pit, with the highest overall average mean ratio found at Saxon pit; the average for Orton pit falls between. The same is also reflected in the initial mean ratios and highest mean ratios. However, Saxon pit has the lowest final mean ratio, although this mean ratio

has only a sample size of 3 and it is possibly somewhat misleading, see Section 7.4.3.2 and Figure 7.34. The final mean ratio for Calvert pit shows a large increase from its initial mean ratio (the former being its highest mean ratio in this pit as well). At Orton pit there is little change from the initial mean ratio and the final mean ratio.

7.4.2 Results after individual horizons were checked for allometric growth

7.4.2.1 Calvert pit

Figure 7.36 illustrates the result of allometric testing, for Calvert pit, with horizons with $n > 27$ (Table 7.12). Out of the total 8 horizons tested, 6 were found to be of isometric growth, with the other two horizons showing allometric growth. The horizons with allometric growth (horizons 20 and 23) were adjacent to means samples with isometric growth. Therefore the pattern of growth is considered to be significantly different, although the differences in a 's were still tested (see z values in Table 7.12). One significant difference was found between sample means, using t -tests, between horizons 22-23 (4.4-4.6 m).

Horizon number	a value	Z value	Sample size (n)	Allometric (A) / Isometric (I)	Test for significant difference in a (i.e. z value)
9	0.87	-1.45	34	I	
18	1.08	0.55	37	I	
20	1.21	2.68	36	A	-5.66
21	1.08	0.81	35	I	7.33
22	1.20	1.69	44	I	
23	1.20	2.72	32	A	0
24	1.07	0.82	40	I	7.55
41	1.18	1.21	28	I	

Table 7.12. The type of growth for individual horizons, with $n > 27$, for HL-AL ratio for *M. braamburiensis*, Calvert pit. (Z values are not given when the a value is 1.00, isometric growth, because the test for growth type did not need to be performed on these samples.) The test for significant difference in a values for allometric growth is given as the z value. The z value for the test between adjacent horizons is given against the higher horizon number, i.e. the z value for the test between horizons 18-20 is given against horizon 20.

7.4.2.2 Saxon pit

Figure 7.37 illustrates the result of allometric testing, for Saxon pit, on horizons with $n > 27$ (Table 7.13). Out of the six horizons tested three showed isometric growth and three showed allometric growth. Where allometric growth was found, adjacent horizons were all found to differ significantly in the pattern of

growth, see z values in Table 7.13. One significant difference was found between horizons, using t -tests, between horizons 10 and 11 (2-2.2 m), which had already been found to differ in the pattern of growth.

Horizon number	a value	Z value	Sample size (n)	Allometric (A) / Isometric (I)	Test for significant difference in a (i.e. z value)
8	1.06	0.57	29	I	
10	1.17	2.52	34	A	-4.86
11	1.61	4.50	42	A	-19.28
12	1.10	1.75	37	I	22.67
13	1.10	1.16	35	I	0.25
14	1.15	2.88	63	A	-2.71

Table 7.13. The type of growth for individual horizons, with $n > 27$, for HL-AL ratio for *M. braamburiensis*, Saxon pit. (Z values are not given when the a value is 1.00, isometric growth, because the test for growth type did not need to be performed on these samples. The test for significant difference in a values for allometric growth is given as the z value. The z value for the test between adjacent horizons is given against the higher horizon number, i.e. the z value for the test between horizons 8-10 is given against horizon 10.

7.4.2.3 Orton pit

Figure 7.38 illustrates the result of allometric testing, for Orton pit, on horizons with $n > 27$ (Table 7.14). All three horizons tested showed allometric growth, with all adjacent horizons changing in the pattern of growth, see z values in Table 7.14. One significant difference between horizons was found, using t -tests, between horizons 13 and 16 (2.6-3.2 m), although these two horizons were already found to differ significantly in growth pattern.

Horizon number	a value	Z value	Sample size (n)	Allometric (A) / Isometric (I)	Test for significant difference in a (i.e. z value)
6	1.31	2.30	57	A	
13	1.14	2.54	45	A	6.49
16	1.25	2.52	40	A	-5.49

Table 7.14. The type of growth for individual horizons, with $n > 27$, for HL-AL ratio for *M. braamburiensis*, Orton pit. (Z values are not given when the a value is 1.00, isometric growth, because the test for growth type did not need to be performed on these samples.) The test for significant difference in a values for allometric growth is given as the z value. The z value for the test between adjacent horizons is given against the higher horizon number, i.e. the z value for the test between horizons 6-13 is given against horizon 13.

7.4.3 Interpretation of patterns from the Hinge Length to Anterior Length ratio for *M. braamburiensis*

7.4.3.1 Calvert pit

Figures 7.33 and 7.36 illustrate the Hinge Length to Anterior Length for *M. braamburiensis* at Calvert pit. Figure 7.33 can be described as part of a lineage that has generally increased in mean ratio from 0.79 to 1.5. Based on this data it can be interpreted that this ratio for this lineage shows a +NMC over the section, with more +NMC during the MSZ and perhaps some net stasis during the MFZ. A change in the pattern of growth was found between horizons 18-20, 20-21, 22-23 and 23-24, at least in the relationship between Hinge Length and Anterior Length. The interpretation is that these changes are evolutionary, because these changes in the pattern of growth occur within the MSZ and therefore it is believed that these changes are more likely to be genetic changes than ecophenotypic. The t-tests also picked out a true shape change in the data, horizons 22-23. All the changes are found within the MSZ. (I feel it is best to omit horizon 5 at 1 m due to an unacceptably low sample population producing a statistically unreliable result.)

The fact that the pattern observed in Figure 7.36 appears so different to that of Figure 7.33, is explained by the removal of all horizons with $n < 28$ in Figure 7.36; Figure 7.39 exhibits growth curves for horizons with a sample size of $n > 15$, which can also indicate shape changes through this section (Table A2.6). The growth curves are more spread out for this ratio and lineage, and show the Hinge Length grew more rapidly than the Anterior Length, with curves progressing from left to right over the graph. Visually horizons 2-3 look like very different growth curves, with different means as do horizons 3-9, 9-13, and 13-15. From horizons 16-39 the growth curves are tightly bunched together, with a similar gradient, thus indicating no significant change between these horizons. Horizons 40-41 are distinctly different with different means, as are horizons 41-42. However, Table A2.6 picks out growth pattern changes, at least in the relationship between Hinge Length and Anterior Length, between horizons 15-17, 17-18, 18-20, 20-21, 22-23, 23-24 and 41-42. These are completely different to the horizons picked out visually to be different in growth pattern. The large differences between growth pattern of horizons 2-3 (see Figure 7.39) and the others picked out visually are probably due to difference in *b*. These

cannot yet be tested for, and therefore only differences in growth pattern shown in Table A2.6 are valid. Note how all but one of the growth pattern changes are within the lower horizon numbers suggesting more significant changes in the MSZ than the MFZ.

T-tests (Table 7.7) indicate a significant difference between samples from the base of the section and the top of the section. There are also significant differences in samples between the base of the section and the top of the MSZ, suggesting +NMC over this zone. However, t-tests indicate no significant difference between samples at the start of the MFZ and the top of section thus suggesting net stasis over this zone.

The blue and red growth curves are more spread out than the rest indicating growth changes during this part of the section (horizons 1-20, most of the MSZ). However, bunching occurs in the black, green and pink curves. This supports the conclusions that +NMC occurs during the MSZ and net stasis occurs during the MFZ. The means also clearly show increases in Hinge Length, with perhaps some clustering around 8 mm Anterior Length and 12 mm Hinge Length.

Overall the trend is of slight +NMC over the whole section due to the +NMC within the MSZ, whereas net stasis prevailed within the MFZ.

7.4.3.2 Saxon pit

Figures 7.34 and 7.37 illustrate the Hinge Length to Anterior Length ratio for *M. braamburiensis* at Saxon pit. (Horizon 39 should be ignored as it appears to be an anomaly due to a small sample size ($n=3$) in Figure 7.34). Figure 7.37 only shows horizons from the MSZ as numbers of this lineage decline during the MFZ within this pit. Only one significant difference between samples was found, using t-tests; however, a change in the pattern of growth was found between horizons 8-10, 10-11, 11-12 and 13-14, all of which are within the MSZ. The change in pattern of growth, at least in the relationship between Hinge Length and Anterior Length, is interpreted to be evolutionary.

Figure 7.40 illustrates growth curves for horizons with sample sizes $n>15$ so that horizons in the MFZ can also be observed (Table A2.7). The majority of growth curves are bunched together within the same area. The green curve lies in a similar area on the graphs to the red and blue curves. The majority of the means are clustered together around 6 mm Anterior Length

and 9 mm Hinge Length. However, Table A2.7 indicates numerous change in growth pattern, mainly between allometric and isometric growth types. Changes in the pattern of growth were picked out between horizons (with $n > 15$): 2-3, 3-5, 5-6, 6-8, 9-10, 10-11, 11-12, 13-14, 14-15, 15-27, 27-29 and 29-33. Note, how visually the growth curves all look extremely similar (Figure 7.40), but testing the pattern of growth found 9 changes within the MSZ, 2 within the MFZ and one between the two zones. This strongly suggests more morphological changes within the MSZ than the MFZ.

T-test were run over the section. From the base of the section to the top of the section there is no significant difference in the samples, (even with horizon 39 being included in the test) (Table 7.7). Between the base of the section and the top of the MSZ there is also no significant difference in samples. Between the base of the MFZ and the end of section (excluding horizon 39) the t-test result shows no significant difference in means. However, the t-test shows significant change between the start of the MFZ and the top of the section when horizon 39 is included. *It is important to note here how results can change when just one mean is included or removed from the data set.* The result of no significant morphological change between the start of the MFZ to the top of the section is probably more realistic as horizon 39 should not be included due to such a low sample size. Although numerous evolutionary changes are indicated within the MSZ (see Table A2.7), none of these are directional, therefore the overall pattern is one of net stasis over the whole section.

- 7.4.3.3 Orton pit

Figures 7.35 and 7.38 illustrate the Hinge Length to Anterior Length ratio for *M. braamburiensis* at Orton pit. Previously (Section 7.4.1), Figure 7.35 was described as having virtually identical beginning and end samples (1.42 and 1.41 respectively). One significant difference between adjacent samples (horizons 13-16 within the MSZ) was found in Figure 7.38; however, all three horizons tested were found to be of allometric growth, with significant difference in a , therefore showing a change in pattern of growth. This change in the pattern of growth is interpreted to be evolutionary.

As Orton pit only has part of the Peterborough Member a t-test was run from the base of the section to the top, which is identical to the base of the pit

to the top of the MSZ. This showed no significant difference in samples between the base and top of the section. Figure 7.35 does show some morphological change over the section up to horizon 18. (Horizon 19, the last horizon, shows a definite reversal). The t-test result from the beginning of the section to horizon 18 (0-3.4 m) was $P=0.052$. A result of 0.050 or less shows a significant difference, but just one more specimen may make that difference needed. Therefore, according to this strict criterion, there is not quite enough difference between the two mean ratios to consider this a significant change.

Figure 7.41 shows growth curves for horizons with a sample size of $n>13$ (Table A2.8). The blue and red curves overlap, but with the means all fairly well separated, suggesting some shape change. Table A2.8 indicates that there are changes in the pattern of growth, at least in the relationship between Hinge Length and Anterior Length, between horizons 4-6, 8-9, 10-13 and 13-14. Surprisingly the test for differences in a , between horizons 6-8 was found to show no difference in the growth patterns. The curves look distinctly different on Figure 7.41, which is therefore probably due to differences in b . Figure 7.35 does show the samples fluctuating, but with the beginning and end mean ratios being practically identical. Although the t-tests suggested net stasis, this was because the test was comparing the beginning and end two samples. The horizons in Figure 7.38 indicate changes in pattern of growth which are interpreted to be evolutionary, although there is no net directional change.

Therefore, overall, the pattern for this ratio and lineage at Orton pit is one of fluctuating means with no net directional change, with some morphological/shape changes occurring between adjacent samples seen by t-tests, difference in a and the growth curves, but with the beginning and end mean ratios being virtually equal, giving the impression of overall net stasis.

7.5 Hinge Length to Anterior Length for *M. morrisi*

Within this section the microevolutionary patterns of the Hinge Length to Anterior Length ratio for *M. morrisi* from Calvert and Saxon pits are discussed. There are no data from Orton pit for this lineage. Firstly a brief summary is given of the results from both pits, then the results are considered in more detail from each individual pit in turn.

7.5.1 Overview of results

Location	Figure number	Initial mean ratio	Final mean ratio	Lowest mean ratio	Highest mean ratio	Overall average mean ratio for each pit
Calvert	7.42	1.05	2.18	0.99	2.32	1.83
Saxon	7.43	1.99	1.82	1.52	2.38	2.17
Orton	X	X	X	X	X	X

Table 7.15. Mean ratios for HL-AL ratio for *M. morrisi* at all three localities.

This ratio and lineage are illustrated in Figures 7.42 and 7.43, which show completely differing patterns. The initial mean ratio in Calvert pit is considerably lower than that of Saxon pit; and the final mean ratio is considerably higher in Calvert pit than in Saxon pit. However, the overall average mean ratio for Saxon pit is considerably higher than Calvert pit. This is because the mean ratios in Saxon pit are generally larger than in Calvert pit; compare Figure 7.42 with 7.43. For this ratio and lineage Calvert pit shows a large increase in mean ratio from the initial mean ratio to the final mean ratio. Saxon pit shows a decrease in mean ratio from the initial mean ratio and the final mean ratio.

7.5.2 Results after individual horizons were checked for allometric growth

7.5.2.1 Calvert pit

Figure 7.44 illustrates the result of allometric testing, for Calvert pit, on horizons with $n > 27$ (Table 7.16). From the 10 horizons tested, 6 showed isometric growth, the other 4 horizons showed allometric growth. Where allometric growth was found, adjacent horizons were all found to differ significantly in the pattern of growth, see z values in Table 7.16. Four significant differences were found between adjacent horizons, using t-tests, these were: 4-25 (0.8-5.2 m), 26-27 (5.2-5.4 m), 27-28 (5.4-5.6 m) and 32-38 (6.8-7.6 m), although two of these samples (26-27 and 27-28) were found to show allometric growth, previously found as being significantly different in growth patterns.

Horizon number	<i>a</i> value	Z value	Sample size (n)	Allometric (A) / Isometric (I)	Test for significant difference in <i>a</i> (i.e. z value)
4	0.91	-0.72	41	I	
25	0.89	-0.94	35	I	
26	1.29	2.43	56	A	-21.95
27	0.70	-3.16	36	A	29.58
28	1.50	2.86	38	A	-35.90
29	0.81	-2.04	48	A	32.07
30	0.89	-1.26	36	I	-3.88
32	0.87	-1.23	33	I	
38	1.00		45	I	
50	1.00		43	I	

Table 7.16. The type of growth for individual horizons, with n>27, for HL-AL ratio for *M. morrisi*, Calvert pit. (Z values are not given when the *a* value is 1.00, isometric growth, because the test for growth type did not need to be performed on these samples.) The test for significant difference in *a* values for allometric growth is given as the z value. The z value for the test between adjacent horizons is given against the higher horizon number, i.e. the z value for the test between horizons 25-26 is given against horizon 26.

7.5.2.2 Saxon pit

Figure 7.45 illustrates the result of allometric testing, for Saxon pit, on horizons with n>27 (Table 7.17). Out of the 13 horizons tested, 11 were found to have isometric growth and just two horizons were found to have allometric growth. Where allometric growth was found, adjacent horizons were all of isometric growth. Tests showed significant difference in the *a* values, see z values in Table 7.17. No significant differences, using t-tests, between adjacent sample means were found for this ratio and lineage at Saxon pit.

Horizon number	a value	'Z' value	Sample size (n)	Allometric (A) / Isometric (I)	Test for significant difference in a (i.e. z value)
16	1.14	0.88	39	I	
22	1.29	1.56	33	I	
23	1.17	1.17	42	I	7.36
24	1.57	3.52	51	A	-27.07
26	0.86	-1.50	49	I	50.28
34	1.29	1.85	34	I	
35	1.12	0.98	51	I	
38	1.14	1.11	58	I	
39	1.00		57	I	
41	0.81	-1.82	37	I	
42	1.00		33	I	
45	1.13	1.21	18	I	
47	0.75	-2.66	34	A	27.95

Table 7.17. The type of growth for individual horizons, with n>27, for HL-AL ratio for *M. morrisi*, Saxon pit. (Z values are not given when the *a* value is 1.00, isometric growth, because the test for growth type did not need to be performed on these samples.) The test for significant difference in *a* values for allometric growth is given as the *z* value. The *z* value for the test between adjacent horizons is given against the higher horizon number, i.e. the *z* value for the test between horizons 22-23 is given against horizon 23.

7.5.3 Interpretation of patterns from the Hinge Length to Anterior Length ratio for *M. morrisi*

7.5.3.1 Calvert pit

Figure 7.42 illustrates the Hinge Length to Anterior Length for *M. morrisi* at Calvert pit. Previously (Section 7.5.1), it was suggested that Figure 7.42 showed an increase in mean ratio or +NMC over the section. Four places exist where significant differences in the adjacent sample means, using t-tests, were found (Figure 7.44). Only one of these morphological changes occurred within the MSZ, the other three occurred within the MFZ. The significant morphological change within the MSZ (horizons 4-25) was extremely large. This extent of change in morphology was not repeated within the MFZ, which although showing significant morphological change at times, shows a closer approximation to net stasis. The 'a' values of the adjacent horizons found to change in the pattern of growth were also found within the MFZ.

Overall there is a +NMC, with the final mean in the section having shifted positively (by over a mean ratio of 1.0) from the initial point at the base of the section.

The significant differences in adjacent horizons and changes in pattern of growth within the MFZ are at the start of this zone, and this is then followed by a period of samples closer to net stasis (Figure 7.42, 5.6 m-7.4 m). After this period, the samples are generally not as close to net stasis; another significant change in morphology is exhibited (horizons 32-38, Figure 7.44).

Figure 7.46 represents the growth curves for horizons with sample sizes $n > 24$ (Table A2.9). The curves show a trend for more rapid increase in Hinge Length compared to Anterior Length (this is reflected in the progression of the growth curves from the left to the right hand side of the graph). The means are observed to be in an approximate horizontal line, which could suggest that the Anterior Length has stayed virtually the same during the whole section, whilst the Hinge Length has increased; this would give a change in ratio suggesting a shape change. Figure 7.46 shows that there is a large change in growth between the horizons represented by the blue curves and the black curves. The black curves are followed more closely by the green and pink curves. Visually these growth curves show changes in growth style between adjacent horizons: 4-5, 25-26, 26-27, 27-28, 30-31, 31-32, 32-33, and 33-34. Between adjacent horizons 4-5, 25-26, 26-27, and 27-28 the shape change is reflected in change in ratio in Figure 7.42. Most of the visual changes in the pattern of growth curves are picked up by differences in a . Table A2.9 show horizons differing between allometric and isometric growth, as well as allometric growth curves differing significantly. The horizons are: 25-26, 26-27, 27-28, 28-29, 29-30, 30-31, 31-32, 38-49, and 49-50. The only changes picked out by visual examination not shown to differ in a values (horizons 32-33 and 33-34), probably therefore differ in values of b .

The t-test data (Table 7.7) show that there is a significant difference in mean ratios between the base of the section and the top of the section, a pattern of +NMC. There is also a significant difference in mean ratios between the base of the section and the top of the MSZ, illustrating that during the MSZ +NMC occurs. From the start of the MFZ to the top of the section the same t-test result is found suggesting significant morphological change, which was expected as there are significant differences between adjacent samples and pattern of growth between adjacent means during this section. However, between 5.6 and 7.4 m the pattern shown in Figure 7.42 represents a closer approximation to net stasis than morphological change. The t-test between the sample at horizons 28

(5.6 m) and the top of the section ($P=0.096$) revealed that there was no difference in means between these samples; thus a pattern of net stasis can be proposed over this upper part of the MFZ.

Overall the pattern of the data for this ratio and lineage at Calvert pit is one of +NMC; however, from the further t-tests performed it appears that the majority of the +NMC occurred during the MSZ and the beginning of the MFZ, where the pattern of growth changed, whilst net stasis prevailed during the rest of the MFZ.

7.5.3.2 Saxon pit

Figures 7.43 and 7.45 illustrate the Hinge Length to Anterior Length for *M. morrisi* at Saxon pit. Previously (Section 7.5.1), Figure 7.43 was described as having different beginning and end mean ratios; there is much deviation of the other samples but not in any one direction. Figure 7.45 shows horizons with $n>27$; however, no adjacent means were found to show significant differences, using t-tests, although horizons 23-24, 24-26 and 45-47 were found to differ significantly in growth pattern, at least in the relationship between Hinge Length and Anterior Length, which are interpreted to be evolutionary, although these changes are not in any one direction. The numerous shifts in ratio over the section are both positive and negative and create an impression of overall net stasis.

The impression of net stasis, however, is not confirmed by the t-tests, (Table 7.7). From the base to top of section the result shows a significant difference in samples. The t-test result from the base of section to the top of MSZ indicates no significant difference in means. However, the start of the MFZ to the top of section indicates a t-test result of a significant difference in samples. However this t-test result is due to horizon 49, which shows a reversal at the top of section. A t-test was run between the start of the MFZ and horizon 48; the result of $P=0.949$ indicates no significant difference between the samples. This gives the impression of net stasis over the whole studied section.

Figure 7.47 shows growth curves for horizons with a sample size of $n>24$ (Table A2.10). The initial impression is of how different this is compared to the data for Calvert pit (Figure 7.46). All growth curves are very closely bunched and show a high degree of overlap. The means are clustered around 4.5 mm Anterior Length and 10 mm Hinge Length. No other differences in the pattern

of growth were picked out here (see Table A2.10), than were picked out previously in Table 7.17. This confirms the conclusion that this ratio and lineage shows overall net stasis over the whole section, with all negative shifts in morphology cancelling out the positive shifts. (The reversal between horizons 48-49 just being another negative shift in this pattern.)

7.6 Comparison of patterns across all three locations

The patterns detected for the four variates from the two lineages in all three localities (Calvert, Saxon and Orton pits) were illustrated in Sections 7.2-7.5.

Within this section the results from the same ratio and lineage for the three pits are overlain and compared (although for *M. morrisi* there is no data from Orton pit). This allows spatial comparison of the data.

Figures 7.48-7.59 were overlaid by matching the shell bed horizons at the boundary of the *obductum-grossouvrei* Subzone (see previous discussion on correlation, Section 3.5. especially Section 3.5.2).

It had been postulated at the beginning of the study that the data obtained from the three pits would be similar but not necessarily identical. The geographical difference between Calvert pit, Buckinghamshire and Orton pit, Peterborough is 70 km; a further 6 km needs to be added from Orton pit to Saxon pit, Peterborough in a north-easterly direction. Data from pits with geographical separation were chosen to allow observations to be made on the effect geographical separation has on the morphology of the same fauna.

Because of the large geographical separation between pits, there is bound to be some error in overlaying the data and therefore individual sample means cannot be compared; pooled sample means were therefore compared instead.

Within this section the overlaid data is compared visually and using statistical techniques. Visual comparisons of the overlaid data are extremely useful, although often a more useful method of comparison is by employing statistical techniques; this is because such techniques are not biased by preconceptions of patterns in the data and can be used to calculate the degree of confidence in a set of data. T-tests were used to compare the pooled data, although pooled data itself can have an effect on the t-test result. This is due to differences in the number of sample means, and thus sample sizes, in each pooled data group. Therefore two different methods of pooling the data have

been used to try to take into account this effect. The first method used was pooling the data into three groups: Base, Middle and Top. The data were split into these three groups based on visual observations and where a major change often occurred in Figures 7.48-7.59. The second method used was pooling the sample means into two groups based on the MSZ and the MFZ. The pooled data in each group from one pit were then compared, using a t-test, with the same group in another pit.

7.6.1 Length to Height ratio for *M. braamburiensis*

Figures 7.48 and 7.50 illustrate the data overlain for this ratio and lineage at Calvert and Saxon pits; and Calvert, Saxon and Orton pits respectively. (Two sets of figures were used so that all three sets of data did not have to be viewed at the same time.)

Figure 7.48 shows a good match between Calvert and Saxon pits, especially between 4.2 and 4.6 m, where the means are almost identical, and shift together positively and negatively (see Figure 7.49 for just means with sample sizes $n \geq 10$.) The best correlation was expected during the MFZ where the data are closer to net stasis. The red data of Saxon pit are somewhat different, however, from 5.2 m at Calvert pit, and shift positively producing a larger mean ratio during the top half of the data (above the distinctive gap, between 5.4 and 7.6 m). It is not possible to compare the two localities during this period where there are no data.

Figure 7.50, illustrates the same data from Calvert and Saxon pits but with data from Orton pit also overlain. On preliminary examination the points appear to correlate quite well. All the means from all three pits are of approximately the same ratio, with similar length error bars. However, on closer examination of the area 4.2-4.6 m (see Figure 7.51) it is noticeable that the data from Orton pit trend in the opposite direction to the other two localities. Over this part, the means for Calvert and Saxon pits start at 0.98 and shift positively to 1.04 before making a reversal to approximately 0.96 over the 4.2-4.6 m section. However, the data from Orton show that the mean starts at 1.06, then makes a reversal to 0.92, before returning a positive shift to 0.96 over the 4.2-4.6 m interval.

Figure 7.51 shows a clustering together of samples from Calvert and Saxon pits. Overall there is a high degree of correlation of the data from Saxon and Calvert pits for the Length to Height ratio for *M. braamburiensis*, with a low degree of correlation between the data from Orton pit and the other two.

7.6.1.1 Comparison between pits when data are split into three groups

In Section 7.6.1 above the data are compared visually; here the data is split into three pooled groups, Base, Middle and Top. The three groups are split, on Figures 7.48-7.59 as: Base Group, horizons 0-23; Middle Group, horizons 24-41; and Top Group, horizons 42-60. The results of the t-tests for these three groups (Table 7.18) are used to investigate the similarity of data between pits and to compare with visual observations. The t-tests were performed at the 95% confidence level; the null hypothesis is ‘there is no difference between the pooled means of different localities’. To reject the null hypothesis P must be less than 0.05.

	Base Group, (horizons 0-23)		Middle Group, (horizons 24-41)		Top Group, (horizons 42-60)	
	L-H	HL-AL	L-H	HL-AL	L-H	HL-AL
Calvert - Saxon	.910	.000	.481	.000	.078	.241
Saxon - Orton	.709	.001	.871	.000	X	X
Calvert - Orton	.789	.000	.633	.665	X	X

Table 7.18. T-test results of comparing the pooled data, split into 3 groups, from the three localities against each other for *M. braamburiensis*. Note: X= where Orton pit cannot be compared, being a much less complete section, only two groups (base and middle) could be compared.

The Length to Height ratio for *M. braamburiensis*, Calvert, Saxon and Orton pit data are all overlain in Figure 7.51. From the t-test results shown in Table 7.18 one must fail to reject the null hypothesis, and suggest that there is no difference between the pooled means of this Base Group between Calvert-Saxon pits, Saxon-Orton pits and Calvert-Orton pits. In the Middle Group the t-test results for all three pits compared with each other (Table 7.18) shows that again the null hypothesis is accepted for all three comparisons and suggests that there is no difference between the pooled means in all three pits. In the Top Group only Calvert-Saxon pits can be compared. Again the t-test suggests failure to reject the null hypothesis. Therefore overall the t-tests for the Length

to Height ratio for *M. braamburiensis* suggests that the pooled means from all three pits do show similarity.

In Section 7.6.1 it was suggested that the data between Calvert and Saxon pit matched well, with data from Orton matching, but not quite so well within the Base and Middle Groups. In the Top Group it was suggested that the data did not match so well, however the t-test result suggests that the pooled means are fairly similar and therefore overall it can be suggested that the data from all three pits for this lineage and ratio matched well.

7.6.1.2 Comparison between pits when data are split into the two zones, MSZ & MFZ

	MSZ		MFZ	
	H-L	AL-hL	H-L	AL-hL
Calvert - Saxon	.592	.000	.075	.000
Saxon - Orton	.962	.010	X	X
Calvert - Orton	.609	.000	X	X

Table 7.19. T-test results of comparing the data, split into MSZ and MFZ, from the three localities against each other for *M. braamburiensis*.

Table 7.19 illustrates t-test results when comparing data from all three pits, split into the two zones.

Using Figure 7.51 again, the results from this statistical test (Table 7.19) are compared with the graphed data for the Length to Height ratio for *M. braamburiensis*. The t-test result of comparing Calvert-Saxon pits indicates acceptance of the null hypothesis for both the MSZ and MFZ. This suggests little difference between the pooled means of Calvert-Saxon pits through the whole section. The T-test results for comparing Saxon-Orton, and Calvert-Orton pits indicate null hypothesis results that there is little difference in the pooled means for the MSZ.

This is the same result reached by the other statistical test in Section 7.6.1.1 and previously when comparing the Figures visually. Thus overall it is suggested that for the L-H ratio for *M. braamburiensis* the pooled means from all three pits match well.

7.6.2 Length to Height ratio for *M. morrisi*

Figure 7.52 illustrates the data overlain for this ratio and lineage at Calvert and Saxon pit. The data appears to match well, especially between 2.6 and 3.2 m, where the data from both pits are close and trend in the same direction of reversal. The data then appear to diverge before returning to closely match at 4.8 m, though sample sizes are small. Between 4.8-6.8 m the data from Calvert pit show net stasis whilst the data from Saxon pit shows more variation. By 6.8 m the trend of the data from the two localities becomes closer together again, and the means lie on top of each other at a ratio of almost 1.8 by 7.6 m (see Figure 7.53). Between 7.6 m and 10.0 m the data from both localities do diverge slightly once more.

Thus the Length to Height ratio for *M. morrisi*, from both localities appears to converge in places, and diverge in others. Closer correlation was expected between 4.8-6.0 m where the greatest fluctuation in environmental conditions occurs, and where both sets of data show net stasis. Overall both pits' data trend in the same direction over the whole section, one of +NMC.

7.6.2.1 Comparison between pits when data are split into three groups

	Base Group (horizons 0-23)		Middle Group (horizons 24-41)		Top Group (horizons 42-60)	
	H-L	AL-hL	H-L	AL-hL	H-L	AL-hL
Calvert - Saxon	.000	.000	.007	.000	.007	.389
Saxon - Orton	X	X	X	X	X	X
Calvert - Orton	X	X	X	X	X	X

Table 7.20. T-test results of comparing the data, split into 3 groups, from the three localities against each other for *M. morrisi*.

Using Figure 7.53, Length to Height ratio for *M. morrisi*, Calvert and Saxon pit, data overlain (mean ratios only with sample sizes $n \geq 10$); the t-test results from Table 7.20 are compared for this ratio and lineage.

In the Base Group the t-test result for Calvert-Saxon pit indicates rejection of the null hypothesis at the highest level ($P = 0.000$). In the Middle and Top Groups the t-test result shows rejection of the null hypothesis as well. Therefore throughout the whole section for the Length to Height ratio for *M. morrisi* there are differences found in the pooled means and thus there is little correlation in the data from the two localities.

Previously (Section 7.6.2) it was suggested that the two sets of data matched well in places, trending in the same direction; but that in other places the data diverged greatly. The t-tests presented in Table 7.20 compare only the pooled means and not the error bars or trends from each pit, and this is thought to account for the lack of similarity identified between the data sets for the two pits. Figure 7.52 does show that the error bars overlap well between the pits, so the conclusions in Section 7.6.2 that the trend of data in each pit is similar with some close correlations between the two data sets is valid. However the t-test results are also valid in suggesting differences between the pooled means of each pit.

7.6.2.2 Comparison between pits when data are split into the two zones, MSZ and MFZ

	MSZ		MFZ	
	H-L	AL-hL	H-L	AL-hL
Calvert - Saxon	.000	.000	.001	.000
Saxon - Orton	X	X	X	X
Calvert - Orton	X	X	X	X

Table 7.21. T-test results of comparing the data, split into MSZ and MFZ, from the three localities against each other for *M. morrisi*.

Using Figure 7.53 the t-test results (Table 7.21) can be compared with the graphed data. For both zones, MSZ and MFZ, the t-test result indicates rejection of the null hypothesis for Calvert-Saxon pits; suggesting a difference in the data from the two localities across both zones. In Section 7.6.2.1 the null hypothesis over all three groups was also rejected, and therefore this t-test confirms these results. However, both sets of t-test conflict with the previous view (Section 7.6.2), where it was suggested that the two sets of data did have some similarities.

On closer examination of the data in Figures 7.52 and 7.53, the individual means of these two data sets do not actually match well, except at 2.6 m, 6.8 m and 9.8 m. However, the error bars overlap well between the two pits, and the overall trend of the data is the same, one of a +NMC. Thus the original suggestion of similarities between the data is correct. The t-tests only suggest that the pooled means do not show much similarity.

7.6.3 Hinge Length to Anterior Length ratio for *M. braamburiensis*

Figures 7.54 & 7.56 illustrate the overlain data for this ratio and lineage for Calvert and Saxon pits; and Calvert, Saxon and Orton pits respectively.

Figure 7.54 shows that the data for this ratio and lineage do not match well between Calvert and Saxon pits; the data from the two pits are very different. Calvert pit has an average mean of 1.29 whereas the average mean of Saxon is 1.65, so the difference between these means is quite substantial. This large difference could be easily explained if the error bars overlapped, but the majority of the error bars do not overlap. Therefore the data suggest that the ratio for this species is considerably larger in Saxon than at Calvert pit. (This will be discussed in greater detail in Section 7.10.) There is some overlap in error bars further up the section in the MFZ; however, full overlap does not occur until the final mean point from Saxon pit.

The final mean point at Saxon pit has caused some controversy, and has frequently been left out of previous interpretations because of the small sample size. This point is regarded as unreliable and omitted. Figure 7.55 shows just the mean ratios overlaid with $n \geq 10$. This figure shows no overlap of the data between Calvert and Saxon pits. Note, however, that the data become closer nearer the top of the section.

Figure 7.56 exhibits the data from the previous figure (Figure 7.55) but with the data from Orton pit overlain. From preliminary examination it appears that the data from Orton pit match with the data from Saxon pit; however, on more detailed examination this is not always the case. The average of the mean from the Orton pit data is 1.59, compared to 1.65 for Saxon pit.

The mean ratios from Orton pit do not overlies the Saxon means (see Figure 7.57); however, the error bars occur in a similar position on the plot to those of Saxon pit (Figure 7.56). Generally the means for Orton pit are slightly lower than Saxon pit; they fall between Saxon and Calvert pit. Some error bars from the Orton data overlap those of the Calvert data, but all the error bars from Orton data overlap with those from the Saxon data.

Therefore overall for the Hinge Length to Anterior Length ratio for *M. braamburiensis*, it appears that the data from each of the three pits are different, with larger ratios from Saxon and Orton pit compared to Calvert pit.

7.6.3.1 Comparison between data when data are split into three groups

The results from Section 7.6.3 (Figure 7.57) above are compared to the t-test results (Table 7.18).

The results for the Base Group between Calvert-Saxon pit indicate rejection of the null hypothesis at the highest level ($P = 0.00$); indicating a difference between the pooled means of the two pits and therefore little match between the data in the Base Group between those two localities. The t-test results also show that the null hypothesis should be rejected in the Base Group between Calvert-Orton data, and between Saxon-Orton pits; suggesting there is a difference in the Base Group between the pooled means in all three pits. In the Middle Group the t-test, for the comparisons of pooled means between Calvert-Saxon pits, and Saxon-Orton pits, indicates rejection of the null hypothesis (at the highest level $P=0.00$). However within this Middle Group the t-test indicates acceptance of the null hypothesis when Calvert-Orton pits are compared; suggesting that there is similarity in the pooled means from these two pits. In the Top Group the t-test suggests acceptance of the null hypothesis, suggesting Calvert-Saxon pits do have some similarity between the pooled means.

The results of the t-tests agree with observations made by visual examination in Section 7.6.3, namely that there was little match between the data of Calvert and Saxon pits until the top of the section. It was also postulated that there was some match between Saxon and Orton pits' data - although the pooled means were not the same the error bars did overlap. The t-test result indicates no similarity between Saxon and Orton pit; however this is to be expected since the t-test only compares the pooled means. Overall the t-test data indicate that there is little similarity between the data of all three pits for this lineage and ratio, which is the same conclusion reached earlier in Section 7.6.3.

7.6.3.2 Comparison between pits when data are split into two zones, MSZ and MFZ

The results from this statistical t-test, presented in Table 7.19, are compared with the graphed data for the Hinge Length to Anterior Length ratio for *M. braamburiensis* (see Figure 7.57).

The t-test results for the MSZ indicate rejection of the null hypothesis when comparing data from Calvert-Saxon, Saxon-Orton and Calvert-Orton pits. The t-test also indicates rejection of the null hypothesis between Calvert-Saxon pits in the MFZ. This suggests there are differences in the pooled means from all three pits through both zones. However, when the data were previously split into three groups the t-test from the Top Group suggested that there was similarity in pooled means between Calvert and Saxon pit. Also a similarity between Calvert and Orton data was suggested by the t-test data for the Middle Group (Table 7.18).

These differences in t-test results show how different statistical results can be obtained from splitting the data into different types of groups.

Therefore it may be concluded that for the Hinge Length to Anterior Length for *M. braamburiensis* none of the pooled means from any of the three pits match *well* with each other. The pooled means are all different, the main difference being the overall larger ratios in the Peterborough pits compared to Calvert pit.

7.6.4 Hinge Length to Anterior Length for *M. morrisi*

Figure 7.58 illustrates the overlain data for this ratio and lineage from Calvert and Saxon pit. At the base there is a large difference in mean between the two localities. Calvert has a mean of approximately 1.25 over horizons 4-16; whilst Saxon pit has a mean of approximately 2.0 over the same horizons. This is an extremely large difference in mean. Over the basal part of the section (0.0-5.0 m) there is little overlap in the error bars between the two localities; however, at 3.4 m the means converge at a ratio of 1.55. Unfortunately, for reasons explained earlier, the mean from Saxon pit should be omitted. This being the case the sudden overlap in data from the two localities disappears until much further up the section at 5.0 m (see Figure 7.59) (over 1.6 m further up the section). After 5.0 m it appears as if the data from Calvert and Saxon become much closer together, with means overlapping at 6.4 m, 7.8 m, and means lying on top of each other at 9.8 m and 10.0 m.

After 3.4 m the trend of the data is the same in both localities, that of a positive morphological shift. However, near the top of the section the data from Calvert pit stops and data from Saxon pit continues but in a different

trend. After 9.8 m where the two pits' means lie on top of each other, data from Saxon suddenly shows a reversal trend for 1.4 m. (Calvert data after 9.8 m also shows a reversal trend, but as the data finishes just 20 cm later at 10 m, it is not possible to tell whether the data from Calvert would have followed the same trend as Saxon pit.) The final data point from Saxon pit, at 11.2 m, has a ratio of 1.85, a substantial reversal from a mean ratio of 2.2 at 10.0 m recorded from both pits.

Therefore for the Hinge Length to Anterior Length ratio for *M. morrisi* the two sets of data from Calvert and Saxon pits show completely different results at the base of the section, the two data sets coming together by 5.2 m and overlapping frequently by the end of the section. It should be noted that Calvert pit shows +NMC during the MSZ and then net stasis during the MFZ. Where the data overlap at 5.2 m Calvert pit has changed from the MSZ to the MFZ and the data are now approaching net stasis. Previously in Section 7.5 above, this ratio and lineage at Saxon pit was shown to illustrate approximate net stasis throughout. Therefore it appears that Saxon pit starts with ratios that continue approximately the same throughout whilst Calvert pit has a much smaller ratio until after its +NMC where it achieves the ratio obtained by Saxon originally. Net stasis then continues like Saxon pit to the top of the section.

7.6.4.1 Comparison between pits when data are split into three groups

Using Figures 7.58 and 7.59, Hinge Length to Anterior Length for *M. morrisi*, this ratio and lineage can be compared using t-tests (Table 7.20).

-In the Base Group the t-test result indicates rejection of the null hypothesis at the highest level ($P = 0.000$), suggesting that there are differences between the pooled means in the Base Group between Calvert-Saxon pit. The Middle Group gives the same t-test result ($P = 0.000$); suggesting there are differences between the pooled means again. However, in the Top Group, the t-test result indicates acceptance of the null hypothesis, suggesting fewer differences between the two sets of pooled means.

These t-test results are extremely close to the observations made by visual examination, where it was suggested that the two sets of data had no correlation at the base of the section, but that by 5.2 m the data points had come together. However, the data did not match well with Calvert pit until 7.8 m. At

5.2 m the data would be classed as the Middle Group, and the t-test reports that there is no correlation at this point. The only place where two means come close together is horizon 25, when a mean from Saxon pit, with a population of just 3, coincides with one from Calvert pit, with a population of 56. It is my interpretation that the t-test result is correct for the Middle Group in this case, the mean with a sample size of 3 should be ignored. Therefore the data does not match well until much further up the section, where the data points would be placed into the Top Group.

The results of the t-tests have added to the previous suggestions of this ratio and lineage, that the data does not match well in the base or middle section of Figure 7.58, but by the top of the pit the data has come together and correlates relatively well.

7.6.4.2 Comparison between pits when data are split into two zones, MSZ and MFZ

The results of the t-test (Table 7.21) are compared with the graphed data for the Hinge Length to Anterior Length for *M. morrisi* (Figure 7.59).

The t-test results show that during both the MSZ and MFZ the null hypothesis is rejected at the highest level ($P=0.00$). This suggests that there is a difference between the two sets of data during both of the two zones. Previously, (Section 7.6.4.1) the null hypothesis was also rejected, as here, for the Base and Middle Group; but for the Top Group it was accepted, indicating that there was a degree of similarity between the pooled means closer to the top of the section.

-Earlier, in Section 7.6.4, it was suggested that there was little correlation at the base of the section, but that the two sets of data came together towards the top of the section during the MFZ. There are three places during the MFZ where individual means overlie each other well: 7.8 m, 9.8 m and 10.0 m. The t-test result here for the MFZ is an amalgamation of the majority of the Middle and Top Groups, which is why the test indicates there is a difference in the pooled means between the two pits. The t-test result is swayed by the means in the middle part of the section (horizons 24-41) which do not match well.

To conclude, a comparison of the Hinge Length to Anterior Length data for *M. morrisi* shows a poor match during the base and middle section;

however, nearer the top of the section the data appear to converge, with some means becoming extremely close.

7.6.5 Summary of Section 7.6

Geographical separation has a profound effect on the morphological patterns observed. The possible reasons for this are discussed later in Section 7.10.

7.7 Different perceptions of patterns, due to different styles of graphing the data

The method by which data are displayed can have a large impact on the perception of patterns. So far the result graphs (Figures 7.18-7.23, 7.27-7.30, 7.33-7.38, and 7.42-7.45) have been displayed in the same style (one graph to an A4 sheet in a landscape view). However, if graphed in portrait style they would appear very different making any shifts in the mean look less marked. This is because in a landscape view the ratio is given the longer axis and metres along the shorter of the two axes. Therefore any shift in mean will be along the x axis and appear to be quite large. However, in portrait style, the x axis is the shorter in length of the two axes, with metres being along the longer axis and therefore elongated in comparison to the ratio on the x axis. Figure 7.60 illustrates a portrait view of Figure 7.42. Comparing Figure 7.42 to Figure 7.60, one can see that Figure 7.60 appears very long and thin, that the net stasis between horizons 28 and 39 appears much clearer in Figure 7.60, whilst the +NMC during the MSZ is clearer within Figure 7.42. One can therefore see that the shape for Figure 7.42 emphasises morphological changes more than Figure 7.60.

7.7.1 Result graphs with means of sample sizes greater or equal to 5

Figures 7.61-7.65 illustrate the result graphs with means of sample sizes greater or equal to 5. In Sections 7.2-7.5 it was often noted that a mean with very few individual specimens was misleading, such as in the case of Figures 7.34 and 7.43. It is therefore appropriate to graph the result graphs again but with all the small sample-sized means removed. Only 5 out of the original 10

graphs needed to be re-graphed as some already had sample sizes all over or equal to 5. The Figures which were re-graphed are: Figures 7.18, 7.28, 7.33, 7.34, and 7.43. The other graphs (with populations greater or equal to 5) which did not require re-graphing were: Figures 7.19, 7.20, 7.27, 7.35, & 7.42.

Figure 7.61, the re-graphed Length to Height ratio for *M. braamburiensis*, Calvert pit, is only slightly different to the original Figure 7.18. Two samples have been removed, the first one at 1 m, makes a change to the graph. If it was in place it would appear at first glance to show a large reversal trend (Figure 7.18); however, without it (Figure 7.61) the trend of the data now appears as a positive mean shift. The second sample to be removed is at 8.6 m which has made no difference to the overall pattern of the data.

Figure 7.62, the re-graphed Length to Height ratio for *M. morrisi*, Saxon pit (Figure 7.28) has had seven samples removed. The seven samples are from the section at 0.2 m, 1 m, 2 m, 2.2 m, 2.4 m, 2.8 m, & 5.8 m. The number of samples with very long error bars has been reduced. The appearance of the +NMC throughout the section is now much clearer. Figure 7.28 shows much variation in the MSZ due to these seven low population mean ratios, Figure 7.62 however gives a clearer picture at first glance.

Figure 7.65, the re-graphed Hinge Length to Anterior Length ratio for *M. morrisi*, Saxon pit has had the same seven samples removed. This is not a coincidence as the two graphs are of the same lineage *M. morrisi*, and come from the same location. Between 0.2 m and 5.8 m, *M. morrisi* was extremely rare, with only a few specimens being found; these specimens were measured for all four variates. There are no longer any large error bars in the MSZ. The overall net stasis pattern for much of the section is now much clearer.

Figure 7.63, the Hinge Length to Anterior Length ratio for *M. braamburiensis*, Calvert pit has had two samples removed. Comparing Figure 7.63 to Figure 7.33 (the two samples removed were from 1 m & 1.4 m, the base of the MSZ) shows the removal of these two samples does not alter the overall trend of the data. However, the large error bars are now removed making the +NMC trend of the data clearer.

Figure 7.64, the Hinge Length to Anterior Length ratio for *M. braamburiensis*, Saxon pit has had just one sample removed - the final sample on the graph at 7.8 m. This sample originally (Figure 7.34) showed a reversal

from a ratio of 1.61 to a ratio of 1.32. The removal of this sample makes the pattern of net stasis clearer (Figure 7.64).

Figures 7.61-7.65 are in some ways less misleading than Figures 7.18, 7.28, 7.33, 7.34, & 7.43, as they represent samples with a sample size of at least 5; this gives means with smaller error bars.

7.7.2 Graphs with only three points, base of Section, top of MSZ / base of MFZ, and top of Section

The main reason for graphing the results diagrams with only three means, Figures 7.66-7.75, is to try and identify the general trend from the initial sample of the section to the end of the MSZ/the beginning of the MFZ and then to the top of the section. This study was aimed at detecting microevolutionary patterns; it is however, only at a worker's discretion at what resolution level the samples are collected. For this study the Oxford Clay was sampled continuously through the sections chosen, grouping the fauna every 20 cm. This is an extremely high resolution, even for a microevolutionary study; most other studies have not sampled at this resolution (e.g. Cheetham 1987 or Johnson 1993). The effect of graphing just three points is to show the results of sampling at a much lower resolution. These can be compared with the results already obtained (Figure 7.18, 7.19, 7.20, 7.27, 7.28, 7.33, 7.34, 7.35, 7.42, and 7.43). Previously t-tests were run between the three points (start of section, end MSZ/start MFZ and top of section) to see the overall trend of the data through the MSZ and the MFZ (Tables 7.18 and 7.20); this previous discussion will be incorporated here. (Note only horizons with a sample size of 5 or greater are used.)

Figure 7.66, depicting three samples for the Length to Height ratio for *M. braamburiensis*, Calvert pit, shows a pattern of net stasis. The t-test data (Table 7.7) confirm this result and previous discussions (Section 7.2) have determined that this ratio and lineage exhibit stasis over the whole section. Although these three points (low level resolution) show the same overall pattern as Figure 7.18, the numerous samples between these points, showing positive and negative shifts in the mean ratio, are not seen. Three other individual nearby points could have been chosen that failed to reveal this.

Figure 7.67, depicting three samples for the Length to Height ratio for *M. braamburiensis*, Saxon pit, shows a pattern of net stasis. This pattern is confirmed by the t-test data (Table 7.18). Previously (Section 7.2), the pattern was determined to be the same; this is shown clearly in Figure 7.19. However, again the numerous positive and negative shifts in mean ratio between the three points cannot be observed.

Figure 7.68, depicting two samples for the Length to Height ratio for *M. braamburiensis*, Orton pit, shows a slight positive shift in the mean ratio to the right over the MSZ. Previously (Section 7.2) it had been determined the overall pattern was net stasis. This was confirmed by the t-test data (Table 7.18). Although the second mean ratio in Figure 7.68 appears to shift in a positive direction, the error bar is so large that the line drawn between the two points on Figure 7.68 is misleading. Overall the pattern is one of net stasis. Figure 7.20 shows the data fluctuating between these two samples with the reversals cancelling out the positive shifts. This is not seen in Figure 7.68; illustrating how a low resolution study will never be able to present the same amount of information that a high resolution study can.

Figure 7.69, depicting three samples for the Length to Height ratio for *M. morrisi*, Calvert pit, shows an overall trend of a +NMC. The t-test results (Table 7.20) confirm this observation; there are significant difference between the samples. At this low sampling resolution, however, one cannot see the close approximation to stasis observed within Figure 7.27 between horizons 24-33. Overall there is a +NMC over the whole section, but the detailed data between is not present, which could make the low resolution interpretation misleading.

Figure 7.70, depicting three samples for the Length to Height ratio for *M. morrisi*, Saxon pit, shows an overall trend of +NMC within the MSZ, and net stasis within the MFZ. Previously (Section 7.3) it was suggested that t-test results (Table 7.20) showed significant difference between samples during the MSZ and no difference between samples during the MFZ, suggesting net stasis. However, Figure 7.62 does shows +NMC within the MSZ and numerous 'zigs and zags', indicating samples were close to stasis during the MFZ. Figures 7.62 and 7.70 illustrate the same overall result - one of +NMC over some of the MSZ and net stasis over the rest of the section. However, the low resolution

sampling misses out all the 'zigs and zags' which are data that, being available, should not be ignored.

Figure 7.71, depicting three samples for the Hinge Length to Anterior Length for *M. braamburiensis*, Calvert pit, shows an overall trend of +NMC during the MSZ and net stasis during the MFZ. This observation is the same as found from Figure 7.63. However, this is still misleading as all detail is lost between the three points.

Figure 7.72, depicting three samples for the Hinge Length to Anterior Length for *M. braamburiensis*, Saxon pit, shows a pattern of negative shift during the MSZ and a slight positive shift in mean during the MFZ. Overall this gives an impression of net stasis. Originally (Section 7.4.3) it was suggested that the pattern in Figure 7.64 was one of net stasis. This was confirmed by the t-test results (Table 7.18). However, the picture shown in Figure 7.72 is misleading; note the first mean ratio (horizon 1) appears to be much larger than the second mean ratio (horizon 16). However, if one looks at Figure 7.64 it can be seen that horizon 1 has the largest mean within this section. Figure 7.64 shows clearly numerous positive and negative shifts cancelling each other out to give a pattern of net stasis. Horizon 16 is a reversal which is soon cancelled out by the next positive shift, and thus gives a misleading impression on Figure 7.72. Overall the pattern observed on Figure 7.72 is of net stasis; this is the same pattern gained from Figure 7.64, but without the detailed record of samples between the three points.

Figure 7.73, depicting two samples for the Hinge Length to Anterior Length for *M. braamburiensis*, Orton pit, shows a pattern of apparent stasis, with the two means being virtually identical. In Section 7.4.3 it was suggested the pattern for this ratio and lineage was net stasis, which was confirmed by the t-test results (Table 7.18). Note on Figure 7.35 how many 'zigs and zags' are present indicating morphological change but not in any one direction. If sampling had stopped at horizon 17, the pattern might not have shown such good net stasis over the section.

Figure 7.74, depicting three samples for the Hinge Length to Anterior Length for *M. morrisi*, Calvert pit, shows an overall trend of +NMC. Previously (Section 7.5.1) it was suggested that the pattern was +NMC during this section. This was also confirmed by the t-test results (Table 7.20). Figure

7.74, however, only shows +NMC over the section whereas Figure 7.42 shows the data between these three samples. In Section 7.5.1 it was noted that there was a period of net stasis during the MFZ (between 5.6-7.4 m). The pattern after 5.6 m is much closer to approximate stasis than the pattern below it. Previously it was suggested that there was more +NMC during the MSZ than the MFZ. Figure 7.74 does not show this as the data between these three samples are missing.

Figure 7.75, depicting three samples for the Hinge Length to Anterior Length for *M. morrisi*, Saxon pit, shows an overall trend to a smaller ratio. The mean ratio at the base of this pit is the largest mean on this Figure. Previously, (Section 7.5.1) it was suggested that the pattern from this section was one of net stasis. Figure 7.65 shows that the data during the MFZ does appear to be in approximate stasis until the end mean ratio, which shows a slight reversal. Figure 7.65 also shows that the second mean ratio (horizon 2) is the largest mean on the Figure. Note that, except for horizons 1 and 50, the extent of the error bars for horizons 2 and 49 encompass all those other horizons. The t-test result indicates that there is no difference in means between the start of the section and the end of the MSZ. However, the t-tests indicate that there is some difference in means between the end MSZ /start MFZ (horizon 16) and the end of the section (horizon 49), suggesting some reversal. Without horizon 49, however, t-testing between horizon 16-48 gives a result of $P=0.949$, indicating acceptance of the null hypothesis that there is no difference between the samples, suggesting net stasis. Figure 7.75 is extremely misleading in showing such a dramatic negative trend. The pattern from most of the section (Figure 7.65) is one of net stasis with numerous positive and negative shifts cancelling each other out. The third sample (horizon 49) on Figure 7.75 is just another negative shift in mean ratio near the top of the section, indicating low resolution sampling can give the wrong impression.

7.7.2.1 Summary

Figures 7.65-7.75 clearly reveal how low resolution sampling can obscure so much of the important data that is seen at high resolution. A better pattern of data can only be seen in the high resolution figures.

7.8 Variation

Variation is an extremely important aspect in evolutionary studies. The plus ça change model predicts that species will tend to show a greater range of morphological variation at any one time within the MSZ than the MFZ.

Standard deviations are used to illustrate the variation within each sample in the form of bars about each mean ratio (i.e. 2 standard deviations were plotted either side of the mean ratio to form a bar). The data is assumed to be normally distributed (see Appendix 3 for histograms of data to show the distributions observed), so that the variance can be calculated. Variance is the averaged squared difference of the observed values from their mean. However, because it involves squared differences, the variance is sensitive to the sample size in each mean (Isaaks & Srivastava 1989, p.20). Due to this the standard deviation (σ) (i.e. the square root of the variance) was used, which is less sensitive to sample size. (It should be noted that, as with means, a better estimate of the standard deviation is achieved when there is a larger sample size.) Figures 7.76-7.85 illustrate the standard deviation graphs for both ratios and lineages in all three localities.

For both ratios (Length to Height ratio and Hinge Length to Anterior Length ratio) and both lineages (*M. braamburiensis* and *M. morrisi*) in all three localities (Calvert, Saxon and Orton pits) the same conclusions on the amount of variation within a sample and between the two zones (MSZ and MFZ) can be drawn. Individual graphs will not be discussed as has been the case in previous sections, as the results are the same for all figures.

Figures 7.76-7.85 illustrate the variation about each sample mean and allow variation change throughout each pit, and between the other pits, to be compared. All the figures show error bars of approximately the same magnitude (thus variation) for the individual ratio and lineage. (e.g. variation is of the same magnitude for the Length to Height ratio for *M. braamburiensis* at Calvert, Saxon and Orton pits). Variation is also observed to be very similar between the two zones (MSZ and MFZ) for all ratios and lineages, and this suggests that there is little difference in variation for these data between the two zones. These conclusions are true for both Length to Height and Hinge

Length to Anterior Length ratios for *M. braamburiensis* at Calvert, Saxon and Orton pits, and for both Length to Height and Hinge Length to Anterior Length ratios for *M. morrisi* at Calvert and Saxon pits.

This is not in accordance with the prediction of the plus ça change model, which predicted more variation within the MSZ compared to the MFZ. The results here show the same amount of variation throughout both the MSZ and the MFZ for both lineages and ratios at both Calvert and Saxon pits.

The other prediction of the plus ça change is that the sample means in the MSZ will vary more widely than those in the fluctuating zone (except initially). Where differences occur this seems to be true in some cases, e.g. Figures 7.27, 7.42 and 7.43.

7.9 Density of Ribs

So far, all data and interpretation have focused on the four measured variates (Length, Height, Hinge Length and Anterior Length). This section concentrates on the Density of Ribs (DR) data and its interpretation. The measurement of DR has been discussed in Section 5.2; the Duff method of measuring the DR was used.

The DR was taken on all left valves of *M. braamburiensis* at all three localities at distances of 5 mm, 10 mm, 15 mm, 20 mm, and 25 mm from the umbo where possible. The average DR was calculated for each horizon separately by dividing the sum of the total number of ribs on each specimen by the number of specimens. The average number of ribs was calculated because different numbers of specimens were collected at different horizons; this then allowed comparisons between horizons and localities to be made. Sample sizes within an individual horizon ranged from 2 to 31, with 13 being the average sample size.

Figures 7.86-7.88 illustrate the DR at Calvert, Saxon and Orton pits. All Figures have been graphed in the same manner: along the *y* axis is the DR, along the *x* axis are the distances at which these DR measurements were taken, i.e., 5 mm, 10 mm, 15 mm, etc. For all three pits the average DR from each horizon was recorded, and then the total number of horizons from each pit were split into groups of three, i.e. horizons 1-3, 4-6, 7-10 etc. The DR of these three horizons were then averaged and plotted on the graph at the relative

distance from the umbo. The DR is plotted (shown by a cross) and the horizon numbers it represents are next to the cross. Black crosses represent horizons from the MSZ, whilst red crosses represent horizons from the MFZ.

7.9.1 Calvert pit

Figure 7.86 illustrates the DR at Calvert pit. Note that the DR systematically increases with distance from the umbo. The DR at 5 mm from the umbo is always under 15; at 10 mm from the umbo the majority of DR are at 15; at 15 mm from the umbo the DR has increased again, with the majority falling around 20 ribs. By 20 mm from the umbo the DR has increased substantially, with a spread of DR from 20 to 30 ribs. At 25 mm from the umbo the majority of horizons fall around 30 ribs counted.

7.9.2 Saxon pit

Figure 7.87 illustrates the DR at Saxon pit. At this pit the number of *M. braamburiensis* decreased rapidly during the MFZ. Overall there were fewer specimens collected here compared to at Calvert pit; this is reflected by fewer crosses on Figure 7.87. No ribs were counted at further distances than 15 mm from the umbo, due to the specimens being broken, or generally smaller. The DR at 5 mm from the umbo is always under 15; at 10 mm from the umbo the DR is around 20; and at 15 mm from the umbo the DR is spread from 22 to near 30. Overall there is a systematic increase in the DR with increasing distance from the umbo.

7.9.3 Orton pit

Figure 7.88 illustrates the DR at Orton pit. At Orton pit *M. braamburiensis* was the most abundant bivalve found. Orton pit, however, has no exposure from the MFZ and therefore there are fewer crosses compared to Calvert pit. The number of crosses is comparable to Saxon pit, Figure 7.87. Note that the number of *M. braamburiensis* at Saxon pit decreased rapidly within the MFZ and therefore the number of specimens found in both Peterborough pits is probably comparable. At 5 mm from the umbo the DR are all under 15 except for horizons 13-15, which falls around 17 DR; this higher DR is recorded here because horizon 14 had an unusually high DR. At 10 mm from the umbo

the majority of DR fall around 17-18. At 15 mm from the umbo there are only 2 crosses, one at 17 and the other at 23. Here too, DR increases with increasing distance from the umbo.

7.9.4 Interpretation

The interpretation of DR can be applied to all three localities, as they all show the same pattern; increasing DR with increasing distance from the umbo. Figure 7.86 (DR for Calvert pit) illustrates this systematic increase clearly. This increase in DR is due to the overall size; the larger the shell the greater distances from umbo can be measured and thus the greater DR are recorded. Figure 7.89 illustrates this linear relationship; horizons 40-42 at Calvert pit are connected with a straight line. There is clearly a direct correlation between the DR and the size of shell. In Saxon pit (Figure 7.87) there were numerous juvenile/smaller specimens that could only be measured at the smaller distances from the umbo (5 and 10 mm), and no greater distances than 15 mm from the umbo were recorded.

If DR data from all three pits is overlain, it can be identified that the DR from Orton and Calvert pits are extremely similar, with the majority of crosses overlying each other, although at three comparable distances (5, 10 & 15 mm from the umbo) Orton pit always has some crosses with higher DR than Calvert pit. Data from Saxon and Calvert pit do not appear to match at the 5, 10 and 15 mm distances. At each of the three distances the DR at Saxon pit is consistently higher than at Calvert pit. This suggests an overall, greater DR recorded on *M. braamburiensis* for the same size specimen at Saxon pit compared to Calvert pit.

Based on these observations, it can be said that higher DR can generally be attributed to a larger shell. However, overlaying the DR graphs of Calvert and Saxon pits, shows that at 5 mm, 10 mm and 15 mm Saxon pit has a consistently higher DR than Calvert pit. Thus suggesting at Saxon pit *M. braamburiensis* grew increasingly more ribs than Calvert pit at the same distance from umbo. One could speculate that this increased number of ribs at Saxon pit is due to either the shells growing more quickly or more slowly; that the rate of growth could have some influence over the DR. We do not know that if the shell either grew more quickly or more slowly it could attain more

ribs. Unfortunately this question cannot currently be answered from this study, however a previous study of this type, by Johnson (1981), showed that density of plical in *Radulopecten vagans* was very low until it had rapidly grown to a certain size (over 10 mm in height), thus suggesting that the high density of ribs found in *M. braamburiensis* could be due to a slow growth rate. The same argument applies to the question of evolutionary change versus ecophenotypic shape change discussed next (Section 7.10). One could look to Recent populations of bivalves for assistance in answering these questions, as the environment in which bivalves live can in some cases have a large control over morphology. One could not possibly distinguish if faster growth or increase rib numbers were non-genetic responses due merely to the environmental influences on an individual bivalve population.

7.10 Evolutionary change or just ecophenotypic change?

The effects of ecophenotypy have already been discussed, generally, in Section 2.7. It is my interpretation that both genotypic and ecophenotypic changes have been detected within this study. Where large morphological changes tend to occur, the environment is relatively stable (MSZ); see Figure 7.42. This suggests that under stable environmental conditions where morphological change has been identified I believe the principal influence on the fauna is likely to be genotypic (i.e. evolutionary) change. The majority of net stasis occurs within the MFZ, suggesting here that the environmental changes had an influence on the species (as predicted by the plus ça change model), but that the environment forced the lineages into approximate stasis rather than into ecophenotypic induced morphological change. The majority of patterns detected from both the MSZ and MFZ for the two species of bivalve are of net stasis; this was expected as the bivalves were from the dynamic shallow shelf, and the plus ça change model predicts 'more stasis (and occasional punctuations) in the shallow water and temperate zones' (Sheldon 1996b, p.209) (see Section 2.2.2).

The overall mean ratio for both ratios and lineages at Saxon pit (especially HL-AL ratio for *M. braamburiensis*, see Figure 7.56) is generally larger than at Calvert pit. This immediately suggests some difference in

environmental conditions between Saxon pit and Calvert pit (70 km distance), and that this difference had an influence on the growth and shape-form taken by both species. The overall biofacies and lithofacies are similar between Saxon and Calvert pits (see chapter 4). There could, however, be slight differences in grain size of the sediment, which in turn could affect the fauna. Macquaker & Howell (in press) have shown there to be small-scale changes in some samples at Saxon pit. These small (micro) differences in sediment (not detectable by eye) require further study of the lithologies in Calvert pit to be confirmed at Calvert pit. This overall larger mean ratio at Saxon pit does not have to be an ecophenotypic response though. Local selection could have caused the overall larger mean ratio. It is quite possible that over the distance of 70 km the environment was considerably different, especially in sea floor bottom conditions. Differences in local environmental conditions could have caused a genetic selection that caused the larger mean ratio in *M. braamburiensis* at Saxon pit. However, ecophenotypic variation cannot be ruled out as the controlling mechanism selecting the larger mean ratio either; one can probably never distinguish between the two.

It should be noted that the argument between ecophenotypic and genetic change is one that cannot currently, based on the data available, be solved within the fossil record. Morris (pers. comm 1997), Reid (pers. comm 1997) & Todd (pers. comm 1997) have all suggested the data collected within this study would be inadequate to determine with certainty whether a significant morphological change was genetic or ecophenotypic. It is my interpretation nevertheless that, based on the current data, the significant morphological changes, detected by t-tests, which occur within the MSZ are genetic in origin. The changes in the pattern of growth within the MSZ are interpreted here also to be genetic changes or evolutionary, because patterns of relative growth commonly have a high degree of genetic determination. It is less clear whether the significant morphological changes and changes in growth pattern are really genetic changes or not, within the MFZ. Although changes in the pattern of growth are usually considered to be genetic in origin, the changes in pattern of growth that occur within the MFZ usually occur within the most fluctuating part of the MFZ, e.g. HL-AL ratio for *M. morrisi*, Calvert pit, Figures 7.44 and 7.46 and Table A2.9. This suggest that perhaps the fluctuating environment

had an influence on the pattern of growth, and perhaps an influence on the changing morphological patterns. It is impossible to answer the question, from this study alone, whether this environmental influence lead to a genetic change or an ecophenotypic change in the growth pattern and morphological patterns.

Taking the overlain data for Calvert and Saxon pits for *M. braamburiensis*, one can see where individual shifts in mean occur together, i.e. in the same direction, e.g. Figure 7.48. Within this Figure shifts in mean occur together between 4.2 and 4.6 m. These sample means all are of isometric growth. In Calvert pit and Saxon pit the shifts between the three sample means are considered to be significant (see Figure 7.21, Calvert pit, horizons 21-31 and Figure 7.22, Saxon pit, horizons 10-12). It has already been suggested that significant differences between sample means within the MSZ are probably genetic. This is the only example within my data where individual significant shifts in sample mean occur in both pits, in the same direction and that are considered to be genetic. All other individual significant shifts in sample mean that have been considered genetic (within the MSZ) and those that cannot be determined as either genetic or non-genetic (within the MFZ) do not match from Calvert pit across to Saxon pit. It is noticeable though, that the one example of genetic shifts in sample means (Figures 7.21 and 7.22) that match across the two pits involves isometric growth.

Unfortunately, with the current data available, one cannot predict whether the overall larger mean ratio of *M. braamburiensis* in the two Peterborough pits is due to local selection or an ecophenotypic response.

7.11 Comparison of this study with the work of Brinkmann

Brinkmann (1929) attempted to penetrate the relationship between time and morphological change. He described geological time as a function of sediment thickness, but the function was unknown. Today we know that sediment thickness is not a direct function of geological time. Macquaker & Howell (in press) (Chapter 4) have recently shown that hiatuses within the Peterborough Member are much more numerous than previously thought. Hiatuses within the Peterborough Member have previously been thought to occur at shell beds (winnowed horizons) and other bed boundaries. Brinkmann (1929, p.58) thought breaks at shell beds represented a break in sedimentation. However, Macquaker & Howell have shown remnant bedding on a millimetre scale which are internally burrowed, suggesting that there are pauses in sedimentation between these beds as well. Therefore hiatuses within the Peterborough Member must occur on a millimetre scale and not the metre scale previously thought. Previously (Section 2.6.1), the accuracy to which Brinkmann recorded the ammonites to the correct stratigraphic level was discussed. We now know that correlating each ammonite to the nearest centimetre was inaccurate due to bed thickness changes across Brinkmann's studied sections which were separated by a distance of 8 km. It is not possible to directly compare the current study to that of Brinkmann's due to the differences in collection resolution. Raup & Crick (1981) re-evaluated Brinkmann's work and illustrated the shell diameter measurements of *Anakosmoceras* and *Zugokosmoceras* at intervals of 100 cm rather than to the centimetre. This interpretation of the results is a more realistic interpretation with which to compare my results.

Brinkmann's amalgamated section at Peterborough is more complete than the section of the Peterborough Member examined within this study; it is important to note which parts of Brinkmann's section match with the section collected for this study at Saxon pit. Brinkmann (1929, p.29-34) described an amalgamated section of the Peterborough area; unfortunately, he did not correlate his section to the ammonite zonation at the time; however, from his descriptions and approximate bed thickness it is relatively easy to correlate his section to mine using bed descriptions. The sharp boundary at 135.5 cm which

Brinkmann (1929, p.30) described as a 'breccia layer, lower part fine coquina in greenish-grey clay, topped by a pavement of broken ammonites' is equivalent to bed JS13; see Figure 3.6. My studied section at Peterborough started 1 m up into bed JS14, and therefore the section of Brinkmann's can only be compared above this breccia layer. Brinkmann's section continues as:

At 135.5 cm Sharp boundary.

390 cm Dark grey, greasy somewhat shaly clay poor in fossils.

410 cm Same clay with *pseudomonotis* shell hash, which gradually becomes commoner.

430 cm Clayey *pseudomonotis* breccia.

450 cm Clay as before, with gradual reduction in *pseudomonotis* shells.

520 cm Dark grey clay as before

530 cm Same clay, again with greater mixture of *pseudomonotis* fragments.

539.5 cm Coarse *pseudomonotis* breccia in clayey matrix grading into a *nucula* bed (mostly bivalved specimens) above. Complete ammonites not uncommon.

At 539.5 cm weakly marked boundary.

540 cm Shell pavement of often well-preserved ammonites.

556 cm Dark grey clay as above, the lower 3 cm with many *Nucula* shells, which quickly grade out upwards.

559.5 cm *Nucula* breccia, developing quickly out of the underlying sediments.

At 559.5 cm clear boundary.

560 cm Shell pavement with ammonites, some well preserved.

680.5 cm Almost black, stiff somewhat shaly clay with some opened bi-valved *Nucula* shells, which become more common toward the base and in the uppermost 10 cm.

At 680.5 cm indistinct boundary.

690 cm *Nucula* breccia in clayey matrix.

740 cm Dark grey clay with some *Nucula* shells, lower boundary sharp, upper boundary indistinct.

759.5 cm Same clay with many shells.

At 759.5 cm weakly marked boundary.

At 135.5 cm the sharp boundary marks the shell bed of bed 13. (All bed numbers within this paragraph correspond to Figure 2.4c, and are after Hudson & Martill 1994, p. 118). The sediment between this sharp boundary and the next boundary at 539.5 cm is equivalent to bed JS14. Between the boundary at 539.5 cm and the clear boundary at 559.5 cm, the sediment thickness is equivalent to beds JS15, JS16, and JS17. Above the clear boundary 559.5 cm and the next boundary at 680.5 cm is Brinkmann's 'black stiff, somewhat shaly clay', equivalent to the 'Dark bed' of Hudson & Martill (1994, p.119); bed number

JS18. Between the indistinct boundary of 680.5 cm and the weakly marked boundary at 759.5 cm is bed JS19, the distinct shell bed, and bed JS20. Above the boundary at 759.5 cm Brinkmann's section continues in the same detail, with numerous breaks until a sharp boundary at 1093.5 cm, which marks the *Acutistriatum* Bed (bed JS38). The rest of Brinkmann's section will not be described in the same detail here, as it is a continuation of the *grossouvrei* Subzone; only the boundaries are noted:

At 759.5 cm weakly marked boundary.

At 793.5 cm clear boundary.

At 854.5 cm sharp boundary.

At 864.5 cm sharp boundary.

At 880.5 cm sharp boundary.

At 895.5 cm sharp boundary.

At 930.5 cm unclear boundary.

At 945.5 cm unclear boundary.

At 990.5 cm poorly marked boundary.

At 1054.5 cm sharp boundary.

At 1093.5 cm sharp boundary.

At 1135.5 cm weakly marked boundary.

The sharp boundary at 135.5 cm is the boundary between the *jason* and *obductum* Subzones; the boundary at 559.5 cm before the 'dark bed' is the boundary between the *obductum* and *grossouvrei* Subzones; and finally the boundary at 1093.5 cm marks the boundary between the *grossouvrei* and *phaeinum* Subzones. The section continues up through the *phaeinum* Subzone until 1310 cm, approximately bed JS43 or JS44 of Hudson & Martill (1994, p.118).

Therefore the studied section at Saxon pit matches most of Brinkmann's section, from 135.5 cm up to just over the boundary at 1093.5 cm. Brinkmann recorded more information within the *jason* Zone than this study (below 135.5 cm). Probably the most important part of Brinkmann's section is between 135.5 cm and the boundary at 680.5 cm. This is equivalent to the whole of the *obductum* Subzone and the boundary at the *grossouvrei* Subzone, and thus the change from the more stable environment to the more fluctuating environment.

7.11.1 Comparison of Brinkmann's data on shell diameter and results of this study

Brinkmann (1929) investigated numerous parameters on the genus *Kosmoceras*. However, the most important is that of shell diameter, which he recorded in detail for all five lineages.

Figure 7.90 shows the parallel evolution of shell diameter in all five of the *Kosmoceras* lineages investigated by Brinkmann, with his breaks/gaps marked as well. On Figure 7.90 one can see that *Zugokosmoceras* starts off very small (60 mm) and increases swiftly to 120 mm by 135 cm. Brinkmann (1929, p.182) assumed a large gap at 135.5 cm due to the presence of a shell bed. Here *Zugokosmoceras* shrank to around 96 mm, and increases about 10-15 mm by level 539 cm. After the gap at 539.5 cm the lineage increased to a maximum diameter of 147 mm at level 793 cm. After this a sudden fall occurs to 130 mm, at which diameter the lineage remains. In the interval 0-135 cm *Anakosmoceras* also grows very quickly from 40-61 mm in diameter. During the gap at 135.5 cm the lineage has a reversal of 11 mm in diameter, then increases slowly in diameter as far as 560 cm, where it attains its maximum of 70 mm diameter. Another reversal is then seen, and the diameter falls to around 55 mm by 855 cm and stays roughly this size until 1300 cm.

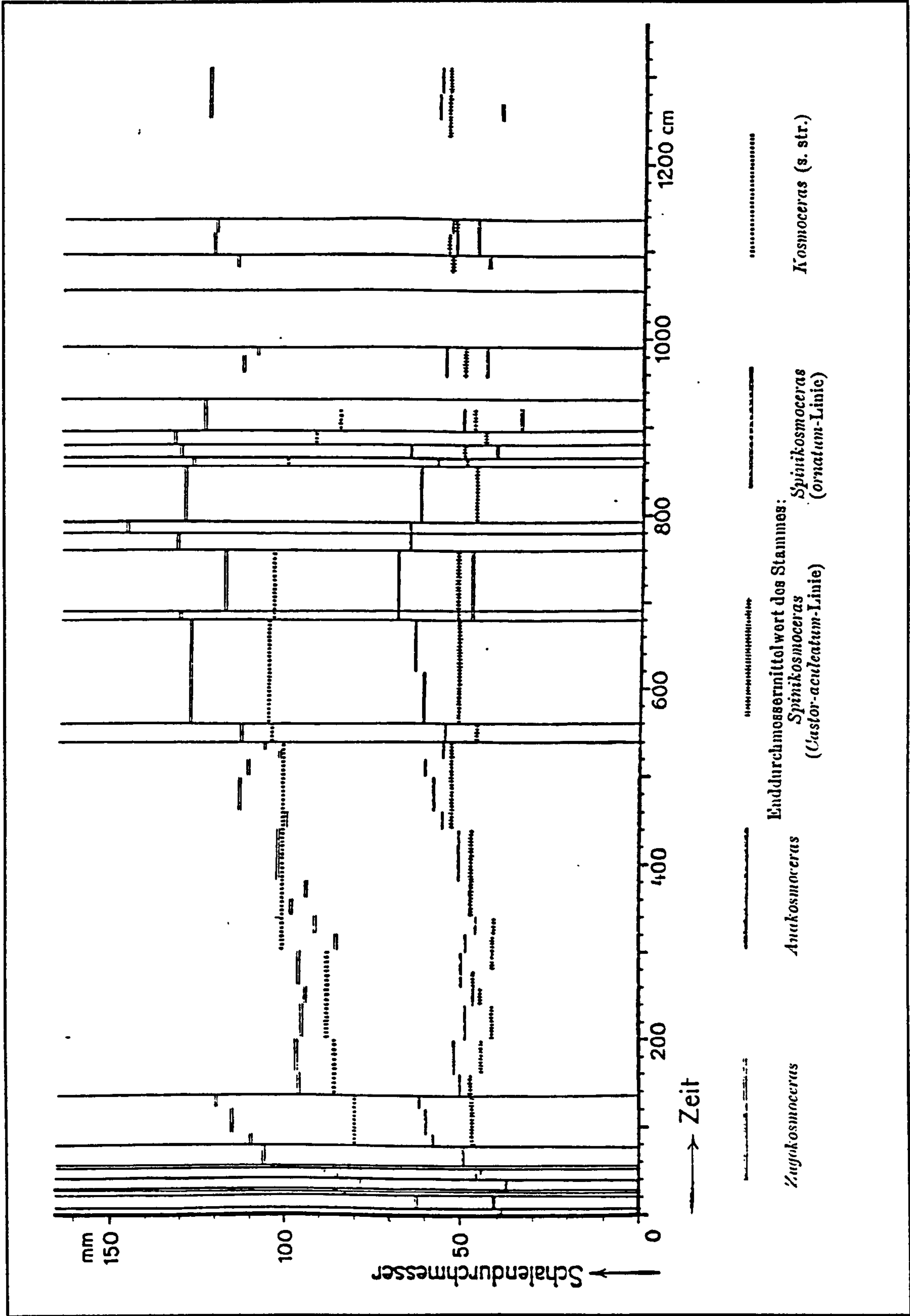


Figure 7.90. Brinkmann's parallel evolution of *Kosmoceras* lineages, From Brinkmann (1929, p.183).

Spinikosmoceras (*castor-aculeatum* branch) increases on the whole as the other two have done by about 8 mm, but does not show the reversal during the gap of 135.5 cm as do the others. The *ornatum* branch, which is poorly represented, deviates from the above-described lineages in decreasing shell size. Brinkmann (1929, p.187) said little of *Kosmoceras* s. str.; its size increases up to around 800 cm, after which a drop may have followed.

Brinkmann (1929, pp.187-188) makes some conclusions about this parallel evolution, including the important remark that there exists 'a very close connection between the sizes of *Zugokosmoceras* and *Anakosmoceras* throughout the investigated period, which cannot possibly be coincidental and in which a high phylogenetic correlation coefficient is expressed'.

The results of this study will be compared to those of *Zugokosmoceras* and *Anakosmoceras* for shell diameter over the section. Raup & Crick (1981, p.204) produced the graphed version of these results on the 100 cm interval (see Figure 7.91a). This graph will be used to compare results.

As the shell diameter is a measure of overall size in *Anakosmoceras* and *Zugokosmoceras*, length of *M. morrisi* and *M. braamburiensis* from Saxon pit, is used to indicate overall size of the bivalves. This has been graphed against Brinkmann's section in centimetres to make comparisons (Figure 7.91b). Brinkmann only collected fossils from the pits around Peterborough; therefore comparisons are made with just my data from Peterborough.

Figure 7.91b for the Length data from *M. braamburiensis*, Figure 7.19 (Length to Height ratio for *M. braamburiensis*, Saxon pit), and Figure 7.64 (Hinge Length to Anterior Length for *M. braamburiensis*, Saxon pit) all show a distinct gap in fauna between 3.2 m and 5.4 m, or the period 535 cm and 755 cm on Brinkmann's section. On Figure 7.91a, both *Anakosmoceras* and *Zugokosmoceras* show net size increase during this period, and therefore what caused the lack of some benthic fauna within this period did not cause a lack of nekton.

Comparing Brinkmann's ammonite size data (Figure 7.91a) to this study's bivalve size data (Figure 7.91b) shows distinctly that in all four lineages a very similar pattern in the size data occurs. Between 150 cm and 650 cm on the section, a net increase in size occurs in both *Anakosmoceras* and *Zugokosmoceras*, with increase in size of *M. morrisi* and *M. braamburiensis*. It

is predicted that *M. braamburiensis* would continue to increase in size until 650 cm, indicated with a P on Figure 7.91b. From 650 cm to 1150 cm decreases in size occurs in *Anakosmoceras*, *Zugokosmoceras* and *M. morrisi*. It is predicted that the mean at 750 cm is a decrease from the predicted mean at 650 cm for *M. braamburiensis*. The boundary between the MSZ and the MFZ is marked on Figure 7.91b; this boundary can be carried over to Figure 7.91a. However, it should be noted that the difference in environment, for substrate conditions, does not have an effect on size.

Size in fossils is notoriously subject to ecophenotypic effects. Here I believe there is a strong case for suggesting that ecophenotypy has had an effect on the size of these four lineages. Evidence for suggesting this is: all four lineages have extremely similar size patterns, even though the two ammonite species have totally different life habits to the bivalves. Therefore change in environment such as food supply, warmth of water, etc. that could have affected both types of fossils (nekton and benthos), and which is strongly linked to the overall size of the lineages, is likely to be the main mechanism controlling the fluctuations in size. One prediction might be that as water became warmer and food supply increased, the overall size of all four lineages increased, although this would have to be fully investigated to be conclusive.

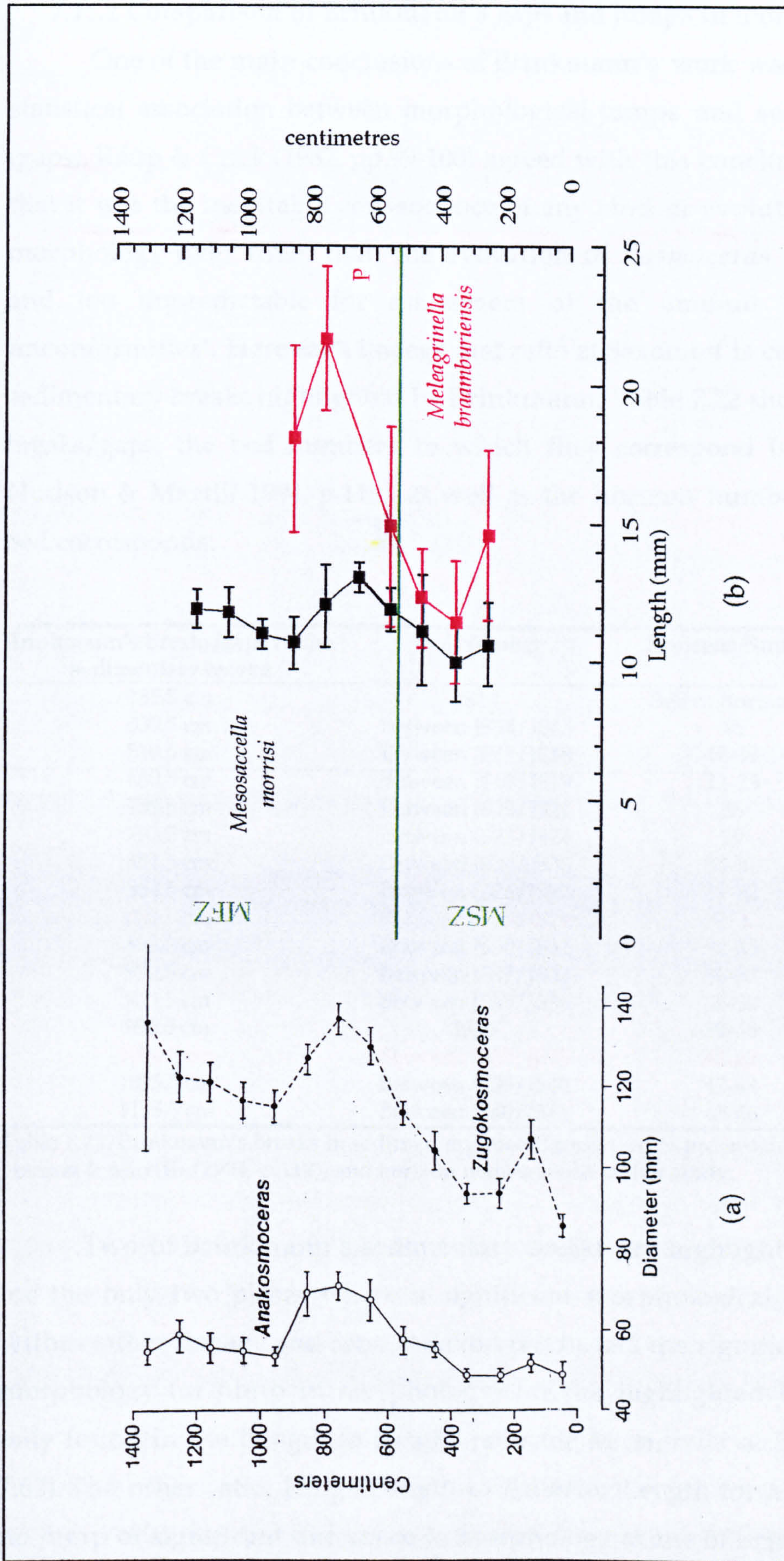


Figure 7.91a and b. (a) Time series for shell diameter of unbroken specimens of *Anakosmoceras* and *Zugokosmoceras*, Peterborough (from Raup & Crick 1981, p.204). (b) Time series for length of unbroken specimens of *Mesosaccella morrisi* and *Meleagrinella braamburiensis*, Saxon pit, Peterborough. Points on both (a) and (b) are sample means for specimens in a 100 cm interval; error bars are four standard deviations. MSZ = more stable zone; MFZ = more fluctuating zone.

7.11.2 Comparison of Brinkmann’s gaps and jumps in morphology

One of the main conclusions of Brinkmann’s work was that there was a statistical association between morphological jumps and sedimentary breaks (gaps). Raup & Crick (1982, pp.99-100) agreed with this conclusion, but thought that it was the inevitable consequence of any kind of evolutionary change in morphology over time; that ‘the evolution of *Kosmoceras* was too irregular and too unpredictable for assessment of the amount of time lost at unconformities’. Here each lineage and ratio at Saxon pit is compared with the sedimentary breaks highlighted by Brinkmann. Table 7.22 shows Brinkmann’s breaks/gaps, the bed numbers to which they correspond (see Figure 3.6 or Hudson & Martill 1994, p.118), as well as the horizon number to which each bed corresponds:

Brinkmann’s breaks/gaps in the sedimentary record	Bed Number	Horizons Number
135.5 cm	JS13	Before horizon 1
539.5 cm	Between JS14/ JS15	15
559.5 cm	Between JS17/ JS18	17-18
680.5 cm	Between JS18/ JS19	22-23
759.5 cm	Between JS20/ JS21	26
793.5 cm	Between JS23/ JS24	29
854.5 cm	Between JS24/ JS25	30-31
864.5 cm	Between JS26/ JS27	31-32
880.5 cm	Between JS28/ JS29	32-33
893.5 cm	Between JS30/ JS31	34-35
930.5 cm	Between JS32/ JS33	36-37
945.5 cm	Between JS35/ JS36	38-39
990.5 cm	JS36	39-40
1054.5 cm	Between JS37/ JS38	41-42
1093.5 cm	Between JS39/ JS40	43-44
1135.5 cm	Between JS40/ JS41	45-46

Table 7.22. Brinkmann’s breaks in sedimentary record compared to present day bed numbers, after Hudson & Martill (1994, p.118), and horizon numbers used in this study.

Two of Brinkmann’s sedimentary breaks are highlighted in red. These are the only two places where a significant morphological change is found within either lineage and ratio at Saxon pit; in fact the significant difference in morphology (or jump in morphology) for the highlighted breaks above are only found in the Length to Height ratio for *M. morrisi* at Saxon pit (Figure 7.62). The other ratio, Hinge Length to Anterior Length for *M. morrisi*, shows no jump or significant difference in morphology at any of Brinkmann’s breaks. The lineage *M. braamburiensis* shows no jumps or significant differences in

either ratio for any of the sedimentary breaks in Table 7.22, (see Sections 7.2-7.5 for previous t-test results).

Of the 16 breaks recorded in the sedimentary succession (Table 7.22), only 2 were found to show any significant morphological change, and these were in just one ratio from one species of the bivalve fauna. This suggests that there is no association between morphological jumps and sedimentary breaks shown from the two bivalve lineages: *M. braamburiensis* and *M. morrisi*. Brinkmann may have found statistical association between morphological jumps in the genus *Kosmoceras* and sedimentary breaks, but this pattern is not repeated in the bivalve fauna.

7.11.3 Summary

The patterns of size for *Anakosmoceras*, *Zugokosmoceras*, *M. morrisi* and *M. braamburiensis* in Figures 7.91a and b clearly show a distinct match in the pattern of size increase and decrease. This is strongly thought to relate to environmental variation and is therefore considered an ecophenotypic effect.

In concluding the association of jumps in ammonite and bivalve morphological change and sedimentary breaks, i.e. Brinkmann's ammonite data compared to this study's bivalve data, there was very little association between the jumps in morphology of two lineages and the sedimentary breaks recorded by Brinkmann. Almost all ammonite jumps in morphological changes occurred when the bivalve fauna did not jump in morphology.

7.12 Summary of chapter 7

Four variates were measured (Length, Height, Anterior Length, and Hinge Length); shape change patterns as well as changes in growth patterns were detected within both the MSZ and MFZ of the Peterborough Member at Calvert and Saxon pits, and within the MSZ at Orton pit. Concluding remarks about these patterns and whether the morphological changes seen are intra-specific variations (i.e. within the species), or whether new species/descendant species can be named, can be read in Chapter 8. However, here one concludes that although numerous changes in the pattern of growth were recorded, indicating possible evolutionary changes, they tended not to show any net directional change in the patterns, e.g. HL-AL ratio for *M. morrisi*, Calvert pit. Therefore the majority of morphological patterns detected were considered to be of net

stasis. Where +NMC occurred it was mainly found within the MSZ (see Table 7.23 for details) These morphological patterns are considered to be in keeping with the predictions of the plus ça change model.

Ratio, species and pit	Base of section to top of MSZ	Base of MFZ (or top of MSZ) to top of section	Total Number of Specimens
L-H ratio for <i>M. braamburiensis</i> , Calvert pit	Net Stasis	Net Stasis	779
L-H ratio for <i>M. braamburiensis</i> , Saxon pit	Net Stasis	Net Stasis	499
L-H ratio for <i>M. braamburiensis</i> , Orton pit	Net Stasis	X	384
L-H ratio for <i>M. morrisi</i> , Calvert pit	+NMC	+NMC with a period of net stasis	844
L-H ratio for <i>M. morrisi</i> , Saxon pit	+NMC	Net Stasis	920
HL-AL ratio for <i>M. braamburiensis</i> , Calvert pit	+NMC	Net Stasis	541
HL-AL ratio for <i>M. braamburiensis</i> , Saxon pit	Net Stasis	Net Stasis	503
HL-AL ratio for <i>M. braamburiensis</i> , Orton pit	Net Stasis	X	358
HL-AL ratio for <i>M. morrisi</i> , Calvert pit	+NMC	Net stasis with +NMC at the beginning of the zone	730
HL-AL ratio for <i>M. morrisi</i> , Saxon pit	Net Stasis	Net Stasis	908
Overall total number of specimens			6466

Table 7.23. Overview of the morphological patterns observed within the two bivalves species within this study. X = no data.

The changes in the Density of Ribs measurements can be directly related to the size of shell, but it is not clear whether changes in Density of Ribs are attributed to evolution or ecophenotypic change. The higher DR within Saxon pit is thought to be either due to local selection due to a differing environment at Saxon pit or an ecophenotypic response, which influenced *M.*

braamburiensis to grow more ribs at a smaller shell size. Unfortunately one cannot distinguish between the two with the data available.

CHAPTER 8

CONCLUSIONS AND FUTURE WORK

Within this chapter the main conclusions of this study will be made in the order that the work appears in the thesis. Possible future work and the recommendations for future work will also be discussed.

8.1 The small-scale heterogeneity in mudstones

- Within the section studied by Macquaker & Howell (in press) (see Figure A2.1), clay-rich mudstones, silt-rich mudstones, shell-pavements and shell-beds were encountered. These formed six broadly upward-coarsening intervals (metre scale). The upward-coarsening successions are composed of clay-rich mudstones at their bases and silt-rich mudstones at their tops. Shell pavements were found in the lower three metres of the successions between the upward-coarsening successions; in contrast shell-beds were found in the upper two metres of the succession between the upward-coarsening intervals.
- Within the upward-coarsening intervals, bioturbated millimetre-scale upward-fining couplets were observed which are now interpreted as beds.
- It is now recognised that storms were probably responsible for the sedimentation, and that beds were only millimetres thick. The observation that the individual beds were colonised strongly suggests that there were significant hiatuses between storm events.
- The variations in lithofacies within the broadly upward-coarsening successions suggest that, even during this section (previously supposed to be uniform), there were significant variations in the relative length of the sediment transport path through time (both vertical and lateral). It is probable that these variations were produced by relative sea-level change.

- The metre-scale stacked, upward coarsening successions are interpreted to be parasequences. The level between the parasequences, where there is rapid sediment fining, are interpreted to be flooding surfaces /parasequence boundaries. The parasequences are interpreted to have been produced by shoaling following rapid deepening.
- Lateral samples collected from closely spaced locations (<0.5 km) indicate that there is significant lateral lithofacies variability. These data, however, are difficult to interpret as bed-thicknesses are very thin, and much of the succession has been partially homogenised by bioturbation, thus it is not possible to determine if at a bed-scale there are lateral facies variations.

8.2 Population study of the two bivalve species

- *M. braamburiensis* and other epifaunal pectinacean bivalves previously thought to have a pendent life form (Duff 1978, pp.15-16) are now thought to have lived on the sea floor. This is supported by: insufficient evidence for the amount of drift wood needed for this lineage, with its large numbers (millions) of individuals, to be attached to; *M. braamburiensis* having a light weight, thin and wide shell adapted to the soft often 'soupy' substrates; and palaeotemperature values from *M. braamburiensis* of 12.7-14.8° C, typical of benthic bivalves (Williams 1988).
- *M. braamburiensis* and *M. morrisi*, epifaunal and infaunal bivalves respectively, are found to be almost mutually exclusive to each other. This suggests that conditions on the sea floor were changeable, allowing different benthos to colonise at different times.
- *M. braamburiensis* was probably adapted to live on the more soft 'soupy' seafloor surfaces and individuals were benthic opportunists, taking advantage of these conditions. *M. morrisi*, an infaunal deposit-feeder, could probably not have burrowed within or through this soupy layer, and therefore colonised firmer substrates.

- *M. braamburiensis* dominated during the *obductum* Subzone at both Calvert and Saxon pits. *M. morrisi* dominated, alternately with *M. braamburiensis*, during the *grossouvrei* and *phaeinum* Subzones at both localities. Thus during the *obductum* Subzone the domination of just *M. braamburiensis* suggested that seafloor conditions were 'soupy' throughout the subzone and therefore relatively stable. The alternation of *M. morrisi* and *M. braamburiensis* during the *grossouvrei* and *phaeinum* Subzones suggests alternations of firmer and softer substrates, and this interval is therefore considered a more fluctuating period of deposition in comparison to the *obductum* Subzone.

8.3 Morphological patterns of the two bivalve species

8.3.1 Relationships of the species studied

It is necessary to consider the relationship between the possible ancestor and possible descendants of each species (*Meleagrinella braamburiensis* and *Mesosaccella morrisi*), and whether the observed changes in morphology are considered large enough to allow a new (sub) species or descendant to be named, before any conclusions regarding the detected morphological patterns can be made.

M. morrisi has a range and occurrence through the Peterborough Member of England, and is very abundant throughout the *jason* to *athleta* Zones at all exposures. According to Duff (1978) it has possible occurrences in the *mariae* Zone in the Weymouth Member of Scarborough, Yorkshire and the Callovian of France (d'Orbigny 1850). The only closely-related species is from the Lias, *Mesosaccella galatea*, which has a similar form to *M. morrisi*, but is shorter anteriorly, has a greater umbonal angle and is less inflated. There is also a difference in the ornamentation between the two species: *M. galatea* is decorated with very fine, regularly-spaced, incised concentric striae, slightly oblique to the growth lines. *M. morrisi*'s ornamentation is of faint commarginal growth lines only (Duff 1978, pp.28-30). Specimens of *M. morrisi* examined within this study have no resemblance to its ancestor, *M. galatea* (i.e. only faint concentric growth lines were seen, no concentric striae), which only occurred within the Lias (Cox 1936, p.465; 1937, p.191).

Duff (1978, p.30) suggests *M. morrisi* is not commonly seen above the *athleta* Zone within England, where the species range stops. Therefore all morphological patterns detected within this study are considered to be within the species *M. morrisi*.

M. braamburiensis has a range and occurrence through parts of the Callovian; it is common in the Kellaways Beds (Lower Callovian) of the Kent coalfield area and Wiltshire. It is abundant throughout the Peterborough Member of England (*calloviense* to *athleta* Zones), and in the Hackness Rock of Yorkshire (*athleta* to *lamberti* Zones) and Kellaways Rock of Yorkshire, the Shales of the Cornbrash, Yorkshire, and the Clynelish Quarry Sandstone of Brora, Sutherland. *M. braamburiensis* is also found in the Callovian of Germany and Russia (Duff 1978, p.61).

M. braamburiensis has close stratigraphical relatives, *Meleagrinnella echinata* from the Cornbrash and *Meleagrinnella ovalis* from the Corallian Beds. *M. echinata* is distinguished by its smaller size (Length up to 20 mm), greater inflation, fewer number of 'wire-like', widely spaced ribs on the left valve, the more elongate and pointed posterior auricle of both valves, and the ornament of the right valve, which is only very slightly smaller than the left valve and has an ornament pattern of up to 16 low, faint very divergent radial riblets (Duff 1978, p.61). *M. ovalis* has several distinguishing features, the hinge line of the left valve is rather longer, the ribbing style consists of densely-packed fine radial riblets on both valves (ribbing on the right valve is particularly well marked), and the concentric elements of ornamentation are much stronger than in *M. braamburiensis* (Duff 1978, p.61). Duff (pers. comm 1997) has suggested that one cannot confidently claim *M. ovalis* is a descendant of *M. braamburiensis* since the environmental conditions in which the two species occur are so different. Furthermore, Duff has suggested that it is too simplistic to assume that because *M. ovalis* is found stratigraphically above *M. braamburiensis* it must be a descendant. Stronger and more direct evidence would be needed to prove this.

It has been established that the range for *M. braamburiensis* is from the Kellaways Beds through to the *athleta* Zone within the brick pits of England; this includes the section of the Peterborough Member sampled within this study (*obductum* to *phaeinum* Subzones). All specimens of *M. braamburiensis*

sampled within this study do not represent the descriptions, given by Duff (1978, p.61), of either *M. echinata* or *M. ovalis*, thus all morphological patterns detected within this study are considered to be within the species *M. braamburiensis*.

For both *M. morrisi* and *M. braamburiensis*, all morphological patterns observed within this study can therefore be said to be intra-specific variations of the species, i.e. microevolutionary patterns.

8.3.2 Length to Height ratio for *M. braamburiensis*

- The Length to Height ratio for *M. braamburiensis* at Calvert pit (Figures 7.18, 7.21, 7.24 & 7.61) exhibited numerous changes in the pattern of growth within the More Stable Zone (MSZ), considered to be evolutionary; however, none were in a net direction. The overall morphological pattern observed was of net stasis throughout both the MSZ and the More Fluctuating Zone (MFZ).
- The Length to Height ratio for *M. braamburiensis* at Saxon pit (Figures 7.19, 7.22 & 7.25) exhibited a few changes in the pattern of growth, of which all were within the MFZ; none were directional. These changes in the pattern of growth cannot be convincingly attributed to evolution as they could have been environmentally induced and therefore equally attributable to ecophenotypic variation. The overall morphological pattern observed was of net stasis throughout both the MSZ and the MFZ.
- The Length to Height ratio for *M. braamburiensis* at Orton pit (Figures 7.20, 7.23 & 7.26) exhibited some changes in the pattern of growth within the MSZ, considered to be evolutionary, however, none were in a net direction. The overall morphological pattern observed was of net stasis throughout the MSZ (no sediment from the MFZ occurs at this locality).

- Overall for the Length to Height ratio for *M. braamburiensis* at all three localities net stasis was shown to be the dominant morphological pattern, from the 1662 specimens studied, see Table 8.1. However, numerous positive and negative shifts in mean ratio occurred throughout all three localities, with the negative shifts cancelling out the positive shifts giving the overall impression of net stasis.

8.3.3 Length to Height ratio for *M. morrisi*

- The Length to Height ratio for *M. morrisi* at Calvert pit (Figures 7.27, 7.29 & 7.31) exhibited an overall trend of positive net morphological change (+NMC). There was +NMC over both the MSZ and the MFZ, but with an identifiable period of net stasis during the most fluctuating part of the MFZ (4.8 m - 5.8 m).
- The Length to Height ratio for *M. morrisi* at Saxon pit (Figures 7.28, 7.30, 7.32 & 7.62) exhibited +NMC over the MSZ and net stasis over the MFZ, with some changes in the pattern of growth between sample means, which cannot be convincingly attributed to evolution.
- Overall, from the 1764 specimens studied, for the Length to Height ratio for *M. morrisi* there is evidence for +NMC in both localities, with net stasis during the MFZ, see Table 8.1.

8.3.4 Hinge Length to Anterior Length ratio for *M. braamburiensis*

- The Hinge Length to Anterior Length ratio for *M. braamburiensis* at Calvert pit (Figures 7.33, 7.36, 7.39 & 7.63) exhibited +NMC over the MSZ with numerous changes in the pattern of growth, believed to be evolutionary, and net stasis during the MFZ.
- The Hinge Length to Anterior Length ratio for *M. braamburiensis* at Saxon pit (Figures 7.34, 7.37, 7.40 & 7.64) exhibited net stasis during both the MSZ and the MFZ, but with numerous changes in the pattern of growth within the MSZ, believed to be evolutionary, but which were not directional.

- The Hinge Length to Anterior Length ratio for *M. braamburiensis* at Orton pit (Figures 7.35, 7.38 & 7.41) exhibited fluctuating sample means with changes in the pattern of growth, believed to be evolutionary, but which were not directional. The overall morphological pattern observed was of net stasis from the beginning of the MSZ to the end of the zone.
- Overall a different evolutionary pattern was observed within the two geographic regions: net stasis was observed from 861 specimens studied within the Peterborough pits, and +NMC and net stasis was observed from 541 specimens studied within Calvert pit, see Table 8.1.

8.3.5 Hinge Length to Anterior Length for *M. morrisi*

- The Hinge Length to Anterior Length ratio for *M. morrisi* at Calvert pit (Figures 7.42, 7.44 & 7.46) exhibited an overall trend of +NMC over both the MSZ and the MFZ, with numerous changes in the pattern of growth at the start of the MFZ; these cannot be convincingly attributed to evolution as they could have also been environmentally induced and therefore equally attributable to ecophenotypic variation. However during the majority of the MFZ (from 5.6 m to top of section) the morphological pattern was shown to be net stasis.
- The Hinge Length to Anterior Length ratio for *M. morrisi* at Saxon pit (Figures 7.43, 7.45, 7.47 & 7.65) exhibited an overall pattern of net stasis during both the MSZ and the MFZ.
- The evolutionary patterns displayed from the two localities for this ratio and lineage are different (although the patterns are the same as observed for the same ratio, but for *M. braamburiensis* above): in the Peterborough pits 730 specimens studied showed net stasis throughout both zones, whilst at Calvert pit 908 specimens studied showed +NMC and net stasis, see Table 8.1.

Ratio, species and pit	Base of section to top of MSZ	Base of MFZ (or top of MSZ) to top of section	Total Number of Specimens
L-H ratio for <i>M. braamburiensis</i> , Calvert pit	Net Stasis	Net Stasis	779
L-H ratio for <i>M. braamburiensis</i> , Saxon pit	Net Stasis	Net Stasis	499
L-H ratio for <i>M. braamburiensis</i> , Orton pit	Net Stasis	X	384
L-H ratio for <i>M. morrisi</i> , Calvert pit	+NMC	+NMC with a period of net stasis	844
L-H ratio for <i>M. morrisi</i> , Saxon pit	+NMC	Net Stasis	920
HL-AL ratio for <i>M. braamburiensis</i> , Calvert pit	+NMC	Net Stasis	541
HL-AL ratio for <i>M. braamburiensis</i> , Saxon pit	Net Stasis	Net Stasis	503
HL-AL ratio for <i>M. braamburiensis</i> , Orton pit	Net Stasis	X	358
HL-AL ratio for <i>M. morrisi</i> , Calvert pit	+NMC	Net stasis with +NMC at the beginning of the zone	730
HL-AL ratio for <i>M. morrisi</i> , Saxon pit	Net Stasis	Net Stasis	908
Overall total number of specimens			6466

Table 8.1. Overview of the morphological patterns observed within the two bivalves species within this study. X = no data.

8.4 Comparing the morphological patterns observed to the plus ça change model

The plus ça change model proposes 'that, over geological timescales (e.g. a million years), gradualism is characteristic of narrowly fluctuating, relatively stable environments. By contrast, net stasis (with occasional punctuations) is expected to prevail in the more unstable environments that dominate the fossil record' (Sheldon 1996b, p.214) (Figures 2.2a & b). The model also predicts continuous, gradualistic evolution on land in the tropics and in the deep sea, and for more stasis (and occasional punctuations) in shallow waters and temperate zones (Sheldon 1996, p.209). In the context of this study more morphological change is therefore expected within the MSZ than the MFZ, but with stasis being the overall predominant pattern (because the bivalves of the Peterborough Member come from the shallow sea).

- All ten morphological patterns observed (Sections 8.3.2-8.3.5) are consistent with the plus ça change model. Four of the morphological patterns closely match patterns proposed by the plus ça change model: gradualism during the more stable environment and stasis during the more fluctuating environment (L-H ratio for *M. morrisoni* at Calvert and Saxon pits; HL-AL ratio for *M. braamburiensis* at Calvert pit; and HL-AL ratio for *M. morrisoni* at Calvert pit, see Table 8.1). The other six also show the general pattern proposed by the plus ça change model of net stasis in shallow waters (L-H ratio for *M. braamburiensis* at Calvert, Saxon and Orton pits; HL-AL ratio for *M. braamburiensis* at Saxon and Orton pits; and HL-AL ratio for *M. braamburiensis* at Saxon pit, see Table 8.1).
- The plus ça change model also suggests 'a greater amplitude of morphological responses in a narrowly fluctuating environment can be expected because selection probably has the chance to act on a greater range of variation tolerated (and perhaps produced) in a stable environment under relaxed selection pressures'. Within this study there were found to be no difference in the amount or amplitude of variation in morphology between the MSZ and the MFZ for either species in either Calvert or Saxon

pit. Therefore the prediction for more morphological variation within the more stable environment was not upheld by this study.

- The overwhelming result of morphological patterns from this study is of net stasis, being observed in each of the two species in all three localities. (This can be said with a high degree of confidence as over 6000 specimens were collected and analysed for this study). This result matches closely the plus ça change model's predictions for shallow marine invertebrates.

8.5 Comparisons of Brinkmann's (1929) work to this study

- Patterns of size change in *Anakosmoceras*, *Zugokosmoceras*, *Meleagrinnella braamburiensis* and *Mesosaccella morrissi* all closely matched each other. It was expected that the ammonite data and the bivalve data would match well because size is notoriously related to environmental factors such as food supply, water temperature etc. It is therefore suggested, that because the size data in all four species are so closely matched, that the size change observed here can be attributed to ecophenotypic variation.
- In comparing the evolutionary jumps in the *Kosmoceras* lineages to the significant morphological changes in the bivalve lineages, two significant morphological changes were found to match Brinkmann's evolutionary jumps (out of a possible 16), but in only one of the two ratios for one of the two bivalve lineages (Length to Height ratio for *M. morrissi*). Therefore no parallel significant morphological changes were found within the two bivalve species, or even between the two ratios for *M. morrissi*. Thus there is not a close relationship between the significant morphological changes observed within the two bivalve lineages and Brinkmann's breaks in succession.
- The difference in lifestyle (nektonic *Kosmoceras*, and benthonic bivalves) could account for differences in the morphological jumps observed. However, if anything, one would expect a closer relationship between jumps in morphology and sedimentary breaks in bivalves than in the ammonites, as the bivalves lie directly on the sea floor.

8.6 Future work

This study has not yet addressed itself to arguably what has become the most important issue of the study; to be able to conclude whether the morphological patterns observed are the result of genuine microevolutionary changes or ecophenotypic variation. However, in order to achieve this aim further work would be required.

In studies conducted previously, some workers have examined evolutionary relationships within a particular genus on a global scale, e.g. Jurassic workers such as Hallam (1975, 1982) and Johnson (1994) have examined *Gryphaea* globally. However within this study, variation between two species within a relatively close geographical distance (70 km) has been examined. It is not possible to examine *M. braamburiensis* and *M. morrissi* globally as they have limited occurrences (see Section 8.3.1); however, there are other exposures of the Peterborough Member within the country that could be studied, e.g. in Wiltshire and Dorset. *M. braamburiensis* is also found in the Callovian of Germany and Russia (Duff 1978, p.61). There is therefore potential for future workers to extend the work presented within this study to provide a wider geographical coverage. The benefits of this wider geographical study would be twofold: (1) it would enable the data and conclusions within this study to be independently validated; (2) it would allow a wider examination of the effect of environmental conditions on shell morphology and therefore help to determine whether the observed changes are ecophenotypic or genetically based.

There are however other options available to allow the two species to be studied further within the brick pits and landfill sites of Peterborough, Bedfordshire and Buckinghamshire; the collected section could be extended. In this study only the *obductum* to base *phaeinum* Subzones were investigated. It may be possible to extend the study into the *jason* Subzone and even further into the *phaeinum* Subzone. This could provide valuable data since the *jason* Subzone is much more fluctuating than the *obductum* Subzone (this observation is based on the numerous different lithologies present within the *jason* Subzone compared to the *obductum* Subzone), whereas the *phaeinum* Subzone is a continuation of the MFZ.

Apart from investigating the lineages from more ammonite Subzones of the Peterborough Member, further pits in the area could be investigated, for example Quest pit in Bedfordshire (grid reference TL 030 420). This pit has large fresh exposures of *jason* to base *phaeinum* Subzones, which would include the same sections studied within Calvert, Saxon and Orton pits, and the extra *jason* Subzone.

The present is often used as 'the key to the past', and Seed (1980, p.35), whose research concentrates on Recent bivalves, indicated that 'one of the most striking feature of bivalve growth is the degree to which it varies with respect to age and environmental conditions'. Seed (1986) has shown that two species of *Mytilus* grown under comparable environmental conditions showed considerable overlap in shell characters which merged until identification of the two species on gross morphology alone became impossible. Seed's work (see Section 2.7 for fuller discussion) has shown that bivalve morphology can only convincingly show evolution when studied on a global scale; this is comparable to the work of Hallam (1975, 1982). Using the work of Seed as 'the key to the past', and adopting the same rationale, the two bivalve lineages *M. braamburiensis* and *M. morrisi* would have to be studied on a global scale to determine whether the morphological patterns detected in this study are genotypic (and therefore evolutionary) or ecophenotypic (and therefore environmentally induced morphological change); however, this is impossible for the reasons given above in section 8.3.1. The further work proposed for studying the lineages throughout their range (i.e. more ammonite Subzones of the Peterborough Member), and over a wider geographical area (from Peterborough to Wiltshire and Dorset across to Germany and Russia) would aid conclusions about genotypic or ecophenotypic variation, but it still might not provide conclusive evidence.

So far, it has been stated that 'the key' to determining whether changes are ecophenotypic or genetically induced is by examining wider geographical areas; there are however, several problems associated with this assuming that studying a species over a wider geographical area will determine whether morphological changes are ecophenotypic variations or real evolutionary changes. The first problem is that local selection can occur and therefore difference in morphological pattern over a larger geographical area cannot just

be ascribed to ecophenotypic variation. Local selection can be both genotypic selection or an ecophenotypic response, i.e. a local change in environmental conditions could induce either a genetic or ecophenotypic morphological change in the bivalve. Another problem is that as geographical separation becomes wider the correlation between two areas becomes less and less accurate. Macquaker & Howell (in press) have already demonstrated how lithofacies change over a distance of 1 km in Peterborough; therefore over larger distances lithofacies will invariably show greater changes. Precise correlation between areas on a larger scale would almost certainly be inaccurate as well.

Within this study upward-fining millimetre scale beds have been observed within the Peterborough Member (Macquaker & Howell in press). These upward-fining beds were probably produced by intermittent storms and have subsequently been modified by bioturbation. Previously beds were thought to occur on a centimetre to metre scale within the member. In the light of this new discovery further work is needed to undertake to:

- Quantify the small-scale (0.01 m) temporal lithofacies variability within a homogeneous mudstone succession.
- Assess how the small-scale temporal lithofacies can be traced laterally on metre to km scale.
- Determine to what extent storms are the dominant sediment transport mechanism.
- Determine what proportion of the sediment record is recorded in these mudstones and where, and on what scale hiatuses are present.

With the data it would then be possible to determine (a) the bed-scale variability within mudstones; (b) whether or not this bed-scale variability can be reliably used for correlation purposes and if not to determine at what scale (in terms of individual beds, bed-sets, or parasequences) realistic lateral correlations can be made; (c) to what extent episodic storm-events dominate the sedimentary record in the studied succession when previously they have

been thought to have been dominated by varying allocthonous and diagenetic processes.

Further work on the mudstones of the Oxford Clay could aid correlation of units across wider geographical areas, by finding correlatable features (as well as the ammonites).

A proposal has been placed with NERC for a post-doctoral-research assistant post to continue the work on the mudstones of the Oxford Clay Formation at Orton pit. Orton pit has a long exposure (>1 km) of Peterborough Member through the *obductum* Subzone. Reconnaissance work has already shown that key surfaces (shell beds) can be traced over the length of the exposure (see Macquaker & Howell in press). It is envisaged that the post-doctoral study would involve tracing the key surfaces along the pit face using an EDM theodolite and photomontages to provide a high-resolution stratigraphic framework. Small-scale temporal lithofacies variability would then be determined by collecting samples every 0.05 m over a 2.0 m succession. Once this has been accomplished, the intermediate-scale (150 m) lateral facies variability would be determined by sampling five locations, in a similar manner, spaced at equidistant intervals along the quarry face. Once this has been completed, small-scale lateral facies variability would be determined by temporally sampling five additional locations, between two of the previous lateral sample sites (approximately 20 m apart). Overall, this sampling methodology would produce approximately 440 discrete samples and would enable both the small-scale temporal and lateral facies variability (on two scales) within the mudstones in this succession to be characterised.

Inevitably, in the sampling strategy outlined above there will be a discontinuous record of the variability present. In order to obtain a precise match between the discrete samples, a continuous resin-strengthened slab over each of the 2 m successions should be collected. This could then be photographed and analysed using optical densitometry so that the key surfaces and samples can be located relative to each other and the samples within each succession directly compared utilising well logging software (Geoquest). Because of their fine grain size, lithofacies analyses would have to be carried out utilising optical and electron optical backscattered electron microscopy techniques (see Macquaker and Gawthorpe 1993). These techniques would

allow quantitative textural and grain size information to be acquired on a submillimetre-scale.

By combining petrographic data with the quantitative grain size data and field descriptions, it should be possible for the rock to be precisely characterised and the variability present to be characterised on bed, bed-set and parasequence scales.

8.7 Recommendations for future work

Numerous questions have arisen from this study; however the two main questions are: (1) to what extent do the data show ecophenotypic variation or evolutionary change and (2) what scale are the beds within the Oxford Clay, and, more importantly, are they correlatable?

The first question is one that palaeontologists have constantly grappled with and often the fossil record cannot answer the question. This study is no exception; at present the data collected within this study cannot satisfactorily answer this question. It has been recommended that future studies explore the wider geographical distribution of the species utilised within this study (perhaps both the UK and Germany), but also extend the study to include parts of the ammonite subzones not investigated within this study (i.e. *jason* Subzones and *phaeinum* Subzone). Greater emphasis should also be placed on the comparison of modern species with that of ancient species. 'The present is the key to the past', but do we possess this 'key' yet?, Seed (per. comm 1997) thinks not, and I must conclude that further work is also required in this area.

Secondly, further work is required with respect to the scale of beds within the Oxford Clay because it has implications for high-resolution stratigraphy. Macquaker & Howell (in press, see Chapter 4) studied lithofacies variability on a 0.01-1.0 km scale at the same level, and concluded that beds were either very thin and therefore the sampling and making of the thin sections were inappropriate, or that there is lateral variability at this scale. Given the former, then bed-scale correlation would be virtually impossible; given the latter the sedimentary processes operating on mud-dominated shelves are locally very variable. Either way more research is needed to determine the nature of temporal and lateral bed, bed-set and parasequence-scale variability within siliciclastic mudstone successions. This may also have

important implications for the work of other high-resolution stratigraphers; if beds are present at a millimetre scale then high-resolution stratigraphers (e.g. Heselbo & Jenkyns 1996) may only be correlating at a parasequence scale, or at best a bed-set scale: do they realise this?

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APPENDIX ONE

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APPENDIX 1. FAUNAL LIST FOR THE
OXFORD CLAY

INVERTEBRATES

BIVALVES

- Amnicardina* (*Amnicardina*) *tenera* (J Sowerby)
Arctica sp.
Bostina buchari (Roemer)
Campylopectes (*Campylopectes*) *auratus* (Schiothorn)
Chesteria (*Chesteria*) *bedfordensis* Duff
Conchionella maccullyi (Morris)
C. mossa (d'Orbigny)
Dacrydium acuta de Loriol
Dicranulites brata (Phillips)
Eutolium (*Eutolium*) *concordium* (Young and Bird)
E. (E.) subciliata (J Sowerby)
Economa timida Fursich & Palmer
Eogera sp.
Gemmaulidion (*Gemmaulidion*) *minimus* (Leckenby)
G. (G.) concinnus (Phillips)
G. (G.) clathratus (Leckenby)
G. (G.) convexicostum *caesalpinii* (d'Orbigny)
Gryphaea (*Bilobysa*) *dilobatus* Duff
G. (B.) laticosta Lamarck
G. (B.) dilatata J Sowerby
Isocyprina (*Isocyprina*) *roederi* Arkell
Isognomon (*Isognomon*) *promittulus* (Arkell)
Lophocytostrocon *marshii* (J Sowerby)
Meleagrinella bramburiana (Phillips)
Mesozoella morrisi (Deshayes)
Modiolus (*Modiolus*) *bipartitus* J Sowerby
Myophorella (*Myophorella*) *regularis* (Seebach)
M. (M.) cavtonensis Duff
Neocrassina (*Preocrassina*) *ungulata* (Lycett)
N. (P.) calvertensis Duff
Neanicella (*Trantscholdia*) *carinata* (Phillips)
N. (T.) phyllis (d'Orbigny)
Nuculoma pallus (d'Orbigny)
N. kathiynae Duff

- Binatisphinctes binatus* (Leckenby)
B. comptoni (Pratt)
B. hamulatus (Buckman)
Cadoceras compressum (Nikitin)
C. durum (Buckman)
C. milaschevici (Nikitin)
Calliphyloceras demidoffi (Rousseau)
Cardioceras (*Cardioceras*) *buckowskii* Maire
C. (C.) cordatum (J Sowerby)
C. (C.) costicardia Buckman
C. (Pavlovcera) *praecordatum* Douville
C. (P.) scarburgense (Young and Bird)
Chamoussetia funifera (Phillips)
Cremoceras crenatum (Bruguere)
C. renggeri (Oppel)
Distichoceras bicosatum (Stahl)
Erymnoceras coronatum (Bruguere)
E. argoviense (Jeannel)
Euxypidoceras acuticostatum (Young and Bird)
E. hancanum (d'Orbigny)
E. douvillei (Collot)
E. hirsutum (Bayle)
Grossouvria (*Grossouvria*) cf. *leptoides* (Till)
G. (G.) sulcifera (Oppel)
G. (Kleniasphinctes) *vernoni* (Young and Bird)
G. (K.) sp. A
G. (K.) sp. B
G. (Poculisphinctes) *poculum* (Leckenby)
Hecticoceras (?*Lunuloceras*) cf. *lugeoni* (de Tystovitch)
H. (Orbignyceras) *pseudopunctatum* (Lahusen)
H. (Putealicer) *bonarellii* de Loriol
H. (P.) puteale (Leckenby)
H. (Sublunuloceras) *lonsdali* (Pratt)
Honeoplanulites cardoti (Petitclerc)
H. difficilis (Buckman)
Indosphinctes patina (Neumayr)
Kosmoceras (*Gulielmiceras*) *jason* (Reinecke)
K. (G.) medea (Callomon)
K. (Kosmoceras) *kuklikum* (Buckman)
K. (K.) spinosum (J. de C. Sowerby)
K. (Lobokosmokeras) *phaeinum* (Buckman)
K. (L.) proniae Teisseyre
K. (Zugokosmokeras) *grossouvrei* Douville
K. (Z.) obductum (Buckman)
K. (Z.) posterior Brinkman
Longaeviceras laminatum (Buckman)
L. placenta (Leckenby)

- L. staffnense* Sykes
Lytoceras adeloides Kudern
Macrocephalites tumidus (Reinecke)
Ochetoceras (*Campylites*) *delmontanum* (Oppel)
O. (Campylites) sp.
Pachyceras (*Pachyceras*) cf. *crassum* Douville
P. (P.) lalandeanum (d'Orbigny)
P. (Torquistes) *leckenbyi* Arkell
Paralidid glabella (Leckenby)
Peltoceras (*Peltoceras*) ex grp. *athleta* (Phillips)
P. (Peltoceraoides) *williamsoni* (Phillips)
P. (Peltomorophites) *hoplophorus* (Buckman)
P. (P.) subtenue (Bean)
Perisphinctes (*Perisphinctes*) sp. A
Pseudopeltoceras chauvinianum (d'Orbigny)
P. fanulium Spath
Quenstedtioceras henrici (R. Douville)
Q. lambergi (J. Sowerby)
?Q. paucicostatum (Lange)
Reineckeia (*Collotia*) cf. *colloitiiformis* (Jeannel)
R. (C.) oxyptychoides Spath
R. (C.) spathi Bourquin
R. (Reineckeia) *anceps* (Reinecke)
Scaphitoides navicula Buckman
Sigaloceras (*Catasigaloceras*) *anterior* (Brinkman)
S. (C.) enodatum (Nikitin)
S. (C.) sp. A
TEUTHOIDS
Belennopsis bessina (d'Orbigny)
Belennopsis depressa (Quenstedt)
Belennotheutis antiquus Pearce
Cylindroteuthis puzosiana (d'Orbigny)
Hibolites hastata Montfort
Lagonibelus beaumontiana (d'Orbigny)
Mastigophora brevipinnus Owen
Pachyteuthis abbreviata (Miller)
?Romanitheutis sp.
Trachyteuthis sp.
NAUTILOID
Paracenoceras calloviense (Oppel)
FORAMINIFERA
Amniobaculites agglutinans (d'Orbigny)
A. coprolithiformis (Schwager)
A. suprajurassica (Schwager)
Brotzenia cf. *nuda* (Terquem)

B. parastelligera Hofker
B. stelligerostata (Bielecka & Pozaryski)
Bullpora rostrata Quenstedt
Citharina flabellata (Guembel)
C. implecata (Schwager)
C. serratorostata (Guembel)
C. tharimella
Citharmella moelleri (Uhlig)
C. nikitini (Uhlig)
Cyclogyra havina (Terquem)
Dentalina bicornis Terquem
D. cuneiformis Terquem & Berthelin
D. digitata Paalzow
D. filiformis (d'Orbigny)
D. guembeli Schwager
D. pseudocommunis Franke
D. torta Terquem
D. turgida Schwager
D. venusta d'Orbigny
Logatidina lassica (Strickland)
Lysionima mosquensis Uhlig
L. nuda Terquem
L. stelligerata (Reuss)
L. stelligerata francanica (Guembel)
L. moelleri Uhlig
L. nikitini Uhlig
L. pseudostylata Barnard
Guadalupea shenlocki (Battenstaedt)
G. ? sp. 2 Lutze
Guatidina para Lalicker
Lagena sp.
Lenticulina ectypa (Loeblich & Tappan)
L. ectypa (L & T) costata Cordey
L. major (Bornemann)
L. muensteri (Roemer)
L. plebeia (Terquem & Berthelin)
L. quenstedti (Guembel)
L. subulata (Reuss)
L. tharimella (Reuss)
L. varians (Bornemann)
Lingulina cernua Terquem
L. longiscata (Terquem)
L. laevissima (Terquem)
L. nodosaria (Terquem)
Margulina batrakensis (Mjathuk)
Margulina ectypa (Loeblich & Tappan)
M. glabra d'Orbigny
Milhamina parassica (Haeusler)
Mithospnella sp.
Nodosaria corallina Guembel
N. hortensis Terquem
N. metensis Terquem
N. opalina Bertenstein
Nubeculinella bigoti Cushman
Ophthalmodium strumosum (Guembel)
O. stufense (Paalzow)
Paal-owella feifei (Paalzow)
Planularia anceps
P. heterana (Guembel)
P. eugenii (Terquem)
P. filosa (Terquem)
P. protracta (Bornemann)
P. suturalis (Terquem)
Pseudolamarckina jensenensis (Uhlig)
Pseudonodosaria humilis (Bornemann)
P. radiata (Barnard)
P. tenuis (Bornemann)
P. vulgata (Bornemann)
Quinqueloculina sp.
Rheophax helveticus (Hausler)
Saraceniaria oxfordiana Tappan
Spirillina infima (Strickland)
Subdellodina sp.
Textularia jurassica (Guembel)
Triplasia acuta Bartenstein & Brand
T. althoffi (Bartenstein)
T. kimeridensis (Bielecka & Pozaryski)
Tristix triangularis Barnard
T. oolithica (Terquem)
Trochammina globigeriniformis (Parker & Jones)
T. squamata Parker & Jones
Vaginula contracta (Terquem)
Verneulinoides tryphera Loeblich & Tappan
COELENTERATES
Protulophila gestroi Roverto
Trochocyathus magnievillianus Michelin
BRYOZOA
Arachnidium smithi (Phillips)
Hyporosopora spp.
Plagioecia sp.
Ropalonaria? *arachne* (Fischer)
Stomatopora spp
BRACHIOPODS
Acanthorhynchia torioli (Rollier)
Aulacothyris bernadina (d'Orbigny)
Cerenthyris? *oxoniensis* (Davidson)
Lingula craneae Davidson
Orbiculoides latissima (Sowerby)
Rhynchonelloidella socialis (Phillips)
ANNELIDS
Genicularia vertebrales (J. de C. Sowerby)
'Serpula' sulcata J. de C. Sowerby
Serpula sp

ARTHROPODS

CRUSTACEANS
Eryma mandelslohi von Meyer
Eryon sublevis Carter
Glyphaea rostrata Carter
G. stricklandi Bean
Goniichirus cristatus Carter
Magila dissimilis Carter
M. leviniana Carter
Mecochirus pearcei Meloy
Pagurus sp.
Pseudastacus? *serialis* Carter
OSTRACODS
Cytherella fullonica Jones and Sherborn
Eucytherura (*Vesticitytherura*) *costaeirregularis* Whatley
E. (V.) scottii Whatley
Galliacocytheridea postrotunda Oertli
Glabbellacythere reticulata Whatley
G. nuda Wienholz
Lophocythere interrupta interrupta Triebel
L. scabra bucki Lutz
Nophrecythere cruciata cruciata (Triebel)
N. cruciata alata (Whatley)
N. cruciata intermedia (Lutze)
N. cruciata oxfordiana (Lutze)
Palaeocytheridea parabakirovi Malz
Pedicythere anterodentina Whatley
Pleurocythere caledonia Whatley
P. borealis carinata Whatley
Praeschuleridea batei Whatley
CHIMAERAS
Brachymylus altidens Woodward
Ischyodus egertoni (Buckland)
Ischyodus beaumonti Egerton
Leptacanthus spp.
Pachymylus leedsi Woodward
ACTINOPTERYGIANS
Aspidorhynchus eodus Egerton
Asthenocormus sp.
Caturus porteri Rayner
Caturus sp.
Coccolepis sp.
TRACE FOSSILS
Mylcelites enameloides Martill
Ophiomorpha sp.
Thalassinoides sp.

VERTEBRATES

ELASMOBRANCHS
Asteracanthus acutus Agassiz
A. ornatissimus Agassiz
Heterodontus sp
Hybodus obtusus Agassiz
Hybodus dawni Martill
Notidanus muensteri Agassiz
Orectoloboides pattersoni Thies
Palaeobranchaelurus bedfordensis Thies
Paracestracion falcifer Wagner
Protospinax mystus Thies
Spathobatus werneri Thies
Sphenodus longidens (Agassiz)

Hypocrotophus philipsi Woodward
Hypocrotonus leedsi Woodward
H. tenuirostris Woodward
Leedsichthys problematicus Woodward
Lepidotes latifrons Woodward
L. leedsi Woodward
L. macrochertus Egerton
Leptidepis macrophthalmus Egerton
Mextarius leedsi Woodward
Oxoceratodus leedsi Woodward
Pholidophorus sp.
Saurapsis longimanus Agassiz
Otoliths

ICHTHYOSAURS

Ophthalmosaurus icenicus Seeley
O. monocharactus Appleby

LONG NECKED PLESIOSAURS

Cryptolichus corymbus (Phillips)
C. richardsoni (Lydekker)
Maracanosaurus belochis Seeley
M. leedsi Seeley
Pachodus seeleyi Andrews

PLIOSAURS

Liopleurodon jerox Sauvage

L. pachydenus (Seeley)
Peloneustes phylarchus (Seeley)
Phosaurus andrewsi Tarlo
Smolestes vorax Andrews

CROCODILES
Mettorhynchus brachyrhynchus Deslongchamps
M. superciliosus Deslongchamps
Steneosaurus darobriensis Andrews
S. leedsi Andrews

DINOSAURS

Callosaurus leedsi (Lydekker)
Cetosauriscus stewarti Charig
Dryosaurus sp.
Eustreptospondylus oxoniensis Walker
Lexovisaurus darobriensis (Hulke)
Metriacanthosaurus parkeri (von Huene)
Ornithomys leedsi Hulke
Sarcolestes leedsi Lydekker

PTEROSAURS

Rhamphorhynchus bucklandi Phillips
R. jessoni Lydekker

APPENDIX 2. LIST OF OXFORD CLAY FOSSIL LOCALITIES

Compiled by David M. Martill

This list is not comprehensive, but includes currently active pits, coastal sites, and a number of sites of historical importance. A few of the active sites have yielded complete skeletons in recent years despite the highly mechanized nature of the workings. Invertebrates are generally abundant at all of the sites.

It will be apparent that most vertebrates from the Oxford Clay have been, and still are, found in the active brick pits. IT CANNOT BE TOO HIGHLY STRESSED THAT THESE WORKINGS ARE PRIVATE PROPERTY, AND ARE DANGEROUS. Permission must always be obtained to visit them, and conditions of entry rigorously observed.

1. Peterborough, Buntings Lane Borrow Pit. Rubbish dump. TL 200957. Kellaways Beds and basal Lower Oxford Clay. Vertebrates reasonably common.
2. Peterborough, Dogsthorpe Brick Pit. Recently abandoned. TF 210020. Kellaways Beds/Lower Oxford Clay Junction, up to *E. coronatum* Zone. Vertebrates reasonably common in basal Lower Oxford Clay. Arthropods abundant in top of *K. jason* Zone and base of *E. coronatum* Zone.
3. Peterborough, Orton Brick Pit. Active. TL 170940. Lower Oxford Clay *K. jason* Zone to *E. coronatum* Zone.
4. Peterborough, Yaxley Brick Pit. Disused. TL 180930. Lower Oxford Clay *K. jason* Zone to basal *P. athleta* Zone. A boulder clay filled glacial channel on the south side of the pit yields abundant derived Middle Oxford Clay fossils.
5. Peterborough, Norman Cross Brick Pit. Disused. TL 175917. Lower and Middle Oxford Clay. *S. calloviense* Zone to high in the *P. athleta* Zone.
6. Whittlesey, Kings Dyke. Numerous disused brick pits at TL 237970, 230975, 243975. Lower Oxford Clay, *S. calloviense* Zone to basal *P. athleta* Zone.
7. Whittlesey, Active brick pit. TL 247975. Lower Oxford Clay, *S. calloviense* Zone to basal *P. athleta* Zone.
8. Whittlesey, Active brick pit. TL 250967. Lower Oxford Clay to base of poorly fossiliferous Middle Oxford Clay.
9. Maxey Gravel Pit. Cambridgeshire. Active. Floor of pit sometimes Lower Oxford Clay, otherwise Cornbrash. TF 135075.
10. Other Gravel pits in north Cambridgeshire, especially near Baston. TF 110130. Floor of pit frequently exposes Lower Oxford Clay, probably *E. coronatum* Zone.

APPENDIX TWO

This appendix illustrates, for the horizons used in sections 7.2-7.5, for growth curves, the means of sample log values, the standard deviations (*slogx* and *slogy*), '*a*', '*b*', '*r*' (correlation coefficient), & '*z*' values as well as the populations (*n*) and growth type for those individual horizons (allometric or isometric). Note, '*Z*' values are not given for true isometric growth ('*a*' = 1) as the test for growth type did not need to be performed. The final column (far right) gives the test for significant difference in *a* values for allometric growth, given as *z* value. The *z* value for the test between adjacent horizons is given against the higher horizons number, i.e. the *z* value for the test between horizons 15-16 is given against horizon 16.

Horizon number	Log H	Log L	Slog y	Slog x	'a' value	'b' value	'r' (correlation coefficient)	'Z' value	n	Allometric (A) / Isometric (I)	Test for significant difference in <i>a</i> (i.e. <i>z</i> value)
2	1.22	1.20	0.18	0.18	1.00	1.05	0.9728		14	I	
9	1.17	1.17	0.21	0.20	1.05	0.87	0.9590	1.42	71	I	
10	1.27	1.28	0.11	0.09	1.22	0.51	0.8616	1.88	28	I	
12	1.32	1.31	0.10	0.09	1.11	0.76	0.8677	1.13	38	I	
13	1.38	1.38	0.12	0.10	1.20	0.53	0.9093	2.34	34	A	-7.62
15	1.24	1.25	0.15	0.12	1.25	0.08	0.9368	3.13	30	A	-3.63
17	1.23	1.24	0.16	0.14	1.14	0.65	0.9308	2.08	37	A	-7.26
18	1.25	1.24	0.13	0.11	1.18	0.61	0.9196	2.49	40	A	-3.10
20	1.24	1.23	0.16	0.15	1.07	0.85	0.9225	1.06	42	I	-72.36
21	1.34	1.33	0.13	0.12	1.08	0.79	0.9248	1.38	47	I	
22	1.32	1.34	0.12	0.12	1.00	0.95	0.8959		52	I	
23	1.27	1.25	0.17	0.16	1.06	0.87	0.9429	1.17	39	I	
24	1.30	1.29	0.14	0.14	1.00	1.02	0.9920		46	I	
40	1.49	1.48	0.12	0.12	1.00	1.02	09459		30	I	
41	1.26	1.25	0.13	0.12	1.08	0.80	0.9377	1.39.	37	I	
47	1.30	1.29	0.16	0.17	0.94	1.22	0.9206	-0.57	12	I	

Table A2.1 The type of growth for individual horizons for *M. braamburiensis*, Calvert pit.

Horizon number	Log H	Log L	Slog y	Slog x	'a' value	'b' value	'r' (correlation coefficient)	'Z' value	n	Allometric (A) / Isometric (I)	Test for significant difference in <i>a</i> (i.e. <i>z</i> value)
1	0.92	0.92	0.21	0.21	1.00	0.00	0.9861		17	I	
2	1.16	1.14	0.20	0.19	1.05	0.92	0.9897	1.39	17	I	
3	1.12	1.12	0.17	0.15	1.13	0.71	0.9630	1.91	20	I	
5	1.14	1.12	0.22	0.20	1.10	0.81	0.9788	1.77	16	I	
6	1.02	1.03	0.25	0.23	1.08	0.79	0.9812	1.95	22	I	
8	0.94	0.93	0.15	0.15	1.00	1.02	0.9793		29	I	
9	1.06	1.07	0.19	0.19	1.00	0.98	0.9655		22	I	
10	1.05	1.03	0.20	0.20	1.00	1.05	0.9575		36	I	
11	1.04	1.06	0.15	0.14	1.07	0.80	0.9531	1.42	42	I	
12	1.08	1.06	0.20	0.20	1.00	1.05	0.9782		37	I	
13	1.10	1.08	0.21	0.21	1.00	1.05	0.9369		35	I	
14	1.05	1.04	0.22	0.21	1.05	0.91	0.9800	1.80	63	I	
15	1.13	1.12	0.17	0.18	0.94	1.18	0.9751	-1.25	22	I	
27	1.28	1.29	0.17	0.13	1.31	0.39	0.9157	2.38	16	A	-20.67
28	1.30	1.30	0.15	0.13	1.15	0.63	0.8307	0.90	15	I	5.55
29	1.37	1.38	0.09	0.07	1.28	0.40	0.9076	2.02	15	A	-5.114
30	1.33	1.34	0.19	0.19	1.00	0.98	0.9619		16	I	17.15
33	1.01	1.02	0.24	0.20	1.20	0.61	0.9309	1.99	19	A	-7.91

Table A2.2 The type of growth for individual horizons for L-H ratio for *M. braamburiensis*, Saxon pit.

Horizon number	Log H	Log L	Slog y	Slog x	'a' value	'b' value	'r' (correlation coefficient)	'Z' value	n	Allometric (A) / Isometric (I)	Test for significant difference in <i>a</i> (i.e. <i>z</i> value)
1	1.14	1.11	0.21	0.20	1.05	0.94	0.9863	1.04	13	I	
4	0.88	0.88	0.18	0.17	1.06	0.88	0.9875	1.51	19	I	
6	0.86	0.87	0.19	0.17	1.12	0.77	0.9592	2.93	64	A	-18.89
8	1.07	1.03	0.10	0.08	1.25	0.61	0.8838	2.10	24	A	-10.79
9	1.04	1.03	0.25	0.25	1.00	1.02	0.9837		27	I	17.83
10	0.87	0.89	0.12	0.10	1.20	0.63	0.9396	2.34	23	A	-15.43
13	1.06	1.06	0.21	0.21	1.00	0.00	0.9715		46	I	16.68
14	1.09	1.08	0.17	0.17	1.00	1.02	0.9715		29	I	
16	1.08	1.08	0.19	0.19	1.00	0.00	0.9267		44	I	

Table A2.3 The type of growth for individual horizons for *M. braamburiensis*, Orton pit.

Horizon number	Log H	Log L	Slog y	Slog x	'a' value	'b' value	'r' (correlation coefficient)	'Z' value	n	Allometric (A) / Isometric (I)	Test for significant difference in <i>a</i> (i.e. z value)
4	0.77	0.95	0.06	0.08	0.75	1.14	0.7864	-3.68	46	A	
5	0.73	0.92	0.09	0.09	1.00	0.65	0.9006		35	I	-24.25
11	0.79	0.98	0.08	0.9	0.89	0.83	0.8464	-1.25	28	I	
13	0.80	1.01	0.06	0.05	1.20	0.39	0.7435	1.34	29	I	
24	0.83	1.05	0.06	0.06	1.00	0.60	0.7829		23	I	
25	0.84	1.07	0.07	0.07	1.00	0.59	0.5547		42	I	
26	0.85	1.07	0.07	0.06	1.17	0.40	0.7206	1.58	59	I	
27	0.85	1.07	0.07	0.08	0.88	0.82	0.4965	-1.05	41	I	
28	0.82	1.05	0.07	0.06	1.17	0.40	0.6719	1.23	41	I	
29	0.84	1.07	0.07	0.08	0.88	0.80	0.8074	-1.67	48	I	
30	0.84	1.07	0.07	0.07	1.00	0.59	0.6430		39	I	
31	0.90	1.11	0.05	0.06	0.83	0.94	0.6439	-1.33	26	I	
32	0.89	1.12	0.06	0.05	1.20	0.35	0.6989	1.38	35	I	
33	0.90	1.12	0.05	0.05	1.00	0.60	0.6354		28	I	
34	0.88	1.13	0.06	0.05	1.20	0.33	0.2939	0.87	25	I	
38	0.86	1.11	0.80	0.08	1.00	0.56	0.8490		45	I	
49	0.85	1.11	0.05	0.05	1.00	0.55	0.8776		25	I	
50	0.83	1.10	0.08	0.07	1.14	0.38	0.6508	1.08	44	I	

Table A2.4 The type of growth for individual horizons for *M. morrisi*, Calvert pit.

Horizon number	Log H	Log L	Slog y	Slog x	'a' value	'b' value	'r' (correlation coefficient)	'Z' value	n	Allometric (A) / Isometric (I)	Test for significant difference in <i>a</i> (i.e. <i>z</i> value)
2	0.84	1.06	0.04	0.07	0.57	1.72	0.7055	-3.53	11	A	
16	0.81	1.06	0.06	0.06	1.00	0.56	0.7547		39	I	-29.79
22	0.88	1.12	0.07	0.06	1.17	0.37	0.7128	1.19	34	I	
23	0.86	1.10	0.05	0.05	1.00	0.57	0.7517		42	I	
24	0.86	1.11	0.07	0.07	1.00	0.56	0.8003		51	I	
26	0.86	1.10	0.07	0.07	1.00	0.57	0.6827		49	I	
27	0.85	1.09	0.07	0.10	0.70	1.22	0.6790	-3.04	27	A	20.13
32	0.81	1.03	0.09	0.08	1.12	0.45	0.9049	1.33	26	I	-24.04
34	0.78	1.04	0.07	0.07	1.00	0.55	0.7829		34	I	
35	0.78	1.02	0.08	0.07	1.14	0.41	0.8786	1.86	52	I	
37	0.79	1.05	0.08	0.08	1.00	0.55	0.8953		25	I	
38	0.78	1.02	0.07	0.06	1.17	0.39	0.7634	1.71	60	I	
39	0.79	1.04	0.07	0.07	1.00	0.56	0.7338		57	I	
41	0.80	1.04	0.90	0.10	0.90	0.73	0.9112	-1.64	37	I	
42	0.81	1.08	0.08	0.09	0.89	0.71	0.72	-1.64	33	I	
45	0.82	1.09	0.06	0.07	0.86	0.77	0.8203	-1.60	30	I	
47	0.83	1.06	0.07	0.07	1.00	0.59	0.7835		34	I	
49	0.80	1.05	0.07	0.07	1.00	0.56	0.7406		28	I	

Table A2.5 The type of growth for individual horizons for *M. morrisi*, Saxon pit.

Horizon number	Log AL	Log HL	Slog y	Slog x	'a' value	'b' value	'r' (correlation coefficient)	'Z' value	n	Allometric (A) / Isometric (I)	Test for significant difference in <i>a</i> (i.e. <i>z</i> value)
2	0.82	0.70	0.20	0.25	0.80	1.82	0.8657	-1.22	6	I	
3	0.82	0.56	0.22	0.26	0.85	2.22	0.9654	-1.80	7	I	
9	0.84	0.88	0.20	0.23	0.87	1.18	0.7970	-1.45	34	I	
13	1.05	1.02	0.11	0.11	1.00	1.07	0.3111		23	I	
15	0.94	1.01	0.12	0.14	0.86	1.19	0.7458	-1.15	21	I	
17	0.89	1.01	0.17	0.12	1.42	0.29	0.7063	2.08	25	A	-17.93
18	0.91	1.00	0.13	0.12	1.08	0.67	0.5332	0.55	37	I	11.33
20	0.90	1.01	0.17	0.14	1.21	0.47	0.9187	2.68	36	A	-5.66
21	1.01	1.13	0.13	0.12	1.08	0.61	0.8249	0.80	35	I	7.33
22	1.02	1.12	0.12	0.10	1.20	0.47	0.7570	1.69	44	I	
23	0.93	1.07	0.18	0.15	1.20	0.44	0.9380	2.72	32	A	0
24	0.96	1.11	0.15	0.14	1.07	0.59	0.8622	0.82	40	I	7.55
40	1.15	1.28	0.14	0.12	1.17	0.45	0.7519	1.11	25	I	
41	0.92	1.04	0.13	0.11	1.18	0.49	0.7375	1.21	28	I	
42	1.08	1.24	0.14	0.10	1.40	0.22	0.8432	2.25	18	A	-8.46

Table A2.6 The type of growth for individual horizons for *M. braamburiensis*, Calvert pit.

Horizon number	Log AL	Log HL	Slog y	Slog x	'a' value	'b' value	'r' (correlation coefficient)	'Z' value	n	Allometric (A) / Isometric (I)	Test for significant difference in <i>a</i> (i.e. z value)
1	0.55	0.79	0.21	0.19	1.10	0.47	0.9271	1.05	17	I	
2	0.79	0.97	0.21	0.18	1.17	0.45	0.8572	1.14	17	I	
3	0.75	0.95	0.18	0.14	1.28	0.34	0.8725	2.00	20	A	-3.34
5	0.77	0.97	0.21	0.19	1.10	0.50	0.9069	0.93	16	I	6.10
6	0.68	0.87	0.25	0.21	1.19	0.44	0.9223	2.02	22	A	-2.95
8	0.57	0.78	0.17	0.16	1.06	0.55	0.8288	0.57	29	I	4.71
9	0.72	0.93	0.20	0.18	1.11	0.49	0.9431	1.44	22	I	
10	0.69	0.87	0.21	0.18	1.17	0.47	0.9431	2.52	3	A	-4.86
11	0.71	0.95	0.21	0.13	1.61	0.15	0.8416	4.50	42	A	-19028
12	0.69	0.93	0.21	0.19	1.10	0.46	0.9437	1.75	37	I	22.67
13	0.73	0.93	0.22	0.20	1.10	0.51	0.8849	1.16	35	I	
14	0.69	0.90	0.23	0.20	1.15	0.45	0.9329	2.88	63	A	-2.71
15	0.77	0.99	0.17	0.14	1.21	0.37	0.9292	1.84	22	I	-3.19
27	0.92	1.13	0.18	0.13	1.38	0.23	0.8442	2.05	16	A	-6.54
29	1.06	1.27	0.09	0.07	1.28	0.27	0.8706	1.83	15	I	3.814
33	0.68	0.90	0.25	0.21	1.19	0.41	0.9620	2.55	18	A	4.19

Table A2.7 The type of growth for individual horizons for HL-AL ratio for *M. braamburiensis*, Saxon pit.

Horizon number	Log AL	Log HL	Slog y	Slog x	'a' value	'b' value	'r' (correlation coefficient)	'Z' value	n	Allometric (A) / Isometric (I)	Test for significant difference in <i>a</i> (i.e. z value)
1	0.76	0.91	0.23	0.17	1.35	0.34	0.8897	1.89	11	I	
4	0.52	0.73	0.16	0.17	0.94	0.68	0.8837	-0.58	18	I	
6	0.53	0.73	0.21	0.16	1.31	0.37	0.6319	2.30	57	A	-9.44
8	0.72	0.87	0.11	0.08	1.37	0.33	0.7659	2.08	24	A	-1.388
9	0.70	0.84	0.26	0.23	1.13	0.56	0.9380	1.73	27	I	10.53
10	0.54	0.74	0.10	0.11	0.91	0.73	0.7227	-0.69	23	I	
13	0.71	0.92	0.24	0.21	1.14	0.46	0.9447	2.54	45	A	-11.22
14	0.78	0.95	0.17	0.15	1.13	0.51	0.9208	1.47	25	I	0.545
16	0.76	0.93	0.20	0.16	1.25	0.39	0.8626	2.52	40	A	-5.41

Table A2.8 The type of growth for individual horizons for HL-AL ratio for *M. braamburiensis*, Orton pit.

Horizon number	Log AL	Log HL	Slog y	Slog x	'a' value	'b' value	'r' (correlation coefficient)	'Z' value	n	Allometric (A) / Isometric (I)	Test for significant difference in <i>a</i> (i.e. <i>z</i> value)
4	0.60	0.60	0.10	0.11	0.91	1.13	0.2288	-0.72	41	I	
5	0.56	0.52	0.12	0.12	1.00	1.10	0.3127		26	I	
25	0.71	0.96	0.08	0.09	0.89	0.72	0.3723	-0.94	35	I	
26	0.68	1.00	0.09	0.07	1.29	0.25	0.5478	2.43	56	A	-21.95
27	0.69	0.90	0.07	0.10	0.70	1.14	0.3395	-3.16	36	A	29.58
28	0.67	0.97	0.09	0.06	1.50	0.16	0.4856	2.86	38	A	-35.90
29	0.67	0.94	0.09	0.11	0.81	0.80	0.4282	-2.04	48	A	32.07
30	0.70	0.98	0.08	0.09	0.89	0.67	0.6412	-1.26	36	I	-3.88
31	0.73	1.02	0.10	0.07	1.43	0.19	0.6683	2.65	26	A	-30.00
32	0.75	1.04	0.07	0.08	0.87	0.69	0.5560	-1.23	33	I	
33	0.75	1.06	0.05	0.06	0.83	0.74	0.3778	-1.32	27	I	
34	0.77	1.06	0.06	0.07	0.86	0.73	0.3477	-1.03	25	I	
38	0.71	1.04	0.08	0.08	1.00	0.47	0.6714		45	I	
49	0.69	1.04	0.09	0.05	1.80	0.06	0.2619	2.59	25	A	-41.34
50	0.70	1.04	0.08	0.08	1.00	0.46	0.6159		43	I	40.80

Table A2.9 The type of growth for individual horizons for *M. morrisi*, Calvert pit.

Horizon number	Log AL	Log HL	Slog y	Slog x	'a' value	'b' value	'r' (correlation coefficient)	'Z' value	n	Allometric (A) / Isometric (I)	Test for significant difference in <i>a</i> (i.e. z value)
2	0.63	1.00	0.06	0.06	1.00	0.43	0.5406		11	I	
16	0.65	0.98	0.08	0.07	1.14	0.34	0.5034	0.88	39	I	
22	0.72	1.04	0.09	0.07	1.29	0.24	0.5946	1.56	33	I	
23	0.72	1.05	0.07	0.06	1.17	0.31	0.5372	1.17	42	I	
24	0.70	1.04	0.11	0.07	1.57	0.12	0.6769	3.53	51	A	-27.07
26	0.69	1.03	0.06	0.07	0.86	0.64	0.6210	-1.50	49	I	50.28
27	0.67	1.03	0.09	0.08	1.12	0.32	0.7254	-1.50	27	I	
32	0.64	0.96	0.09	0.08	1.12	0.36	0.6823	0.78	26	I	
34	0.63	0.97	0.09	0.07	1.29	0.24	0.7228	1.85	34	I	
35	0.60	0.94	0.09	0.08	1.12	0.35	0.5951	0.98	51	I	
37	0.65	0.99	0.09	0.09	1.00	0.46	0.6787		25	I	
38	0.61	0.96	0.08	0.07	1.14	0.33	0.5301	1.11	58	I	
39	0.64	0.97	0.08	0.08	1.00	0.47	0.5932		57	I	
41	0.65	0.98	0.09	0.11	0.81	0.70	0.6656	-1.82	37	I	
42	0.66	1.02	0.09	0.09	1.00	0.44	0.6631		33	I	
45	0.67	1.00	0.08	0.07	1.13	0.34	0.8334	1.21	29	I	
47	0.67	0.97	0.06	0.08	0.75	0.88	0.6810	-2.66	34	A	27.73
49	0.62	0.89	0.09	0.07	1.28	0.30	0.4351	1.26	27	I	-27.52

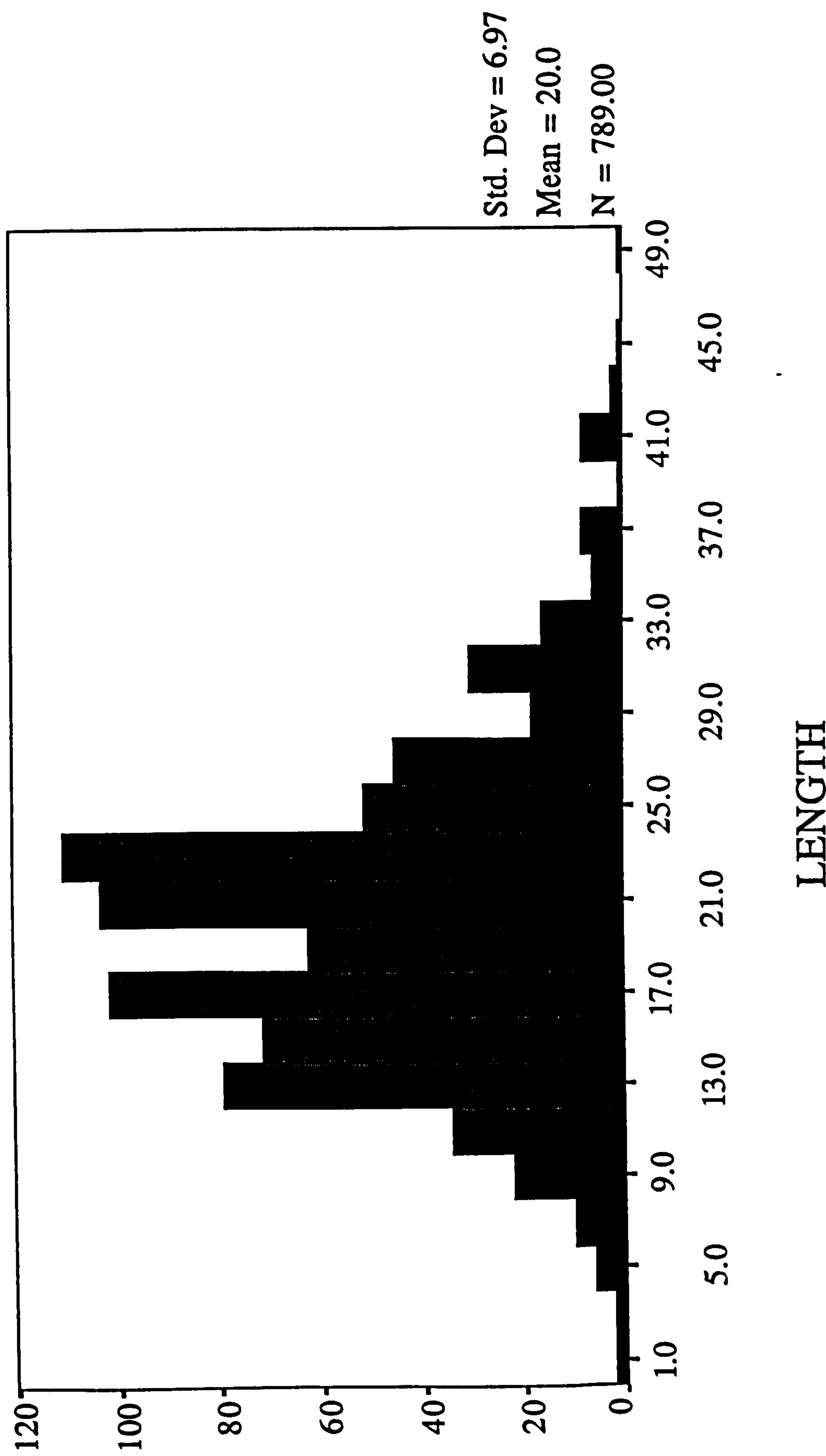
Table A2.10 The type of growth for individual horizons for *M. morrisi*, Saxon pit.

APPENDIX THREE

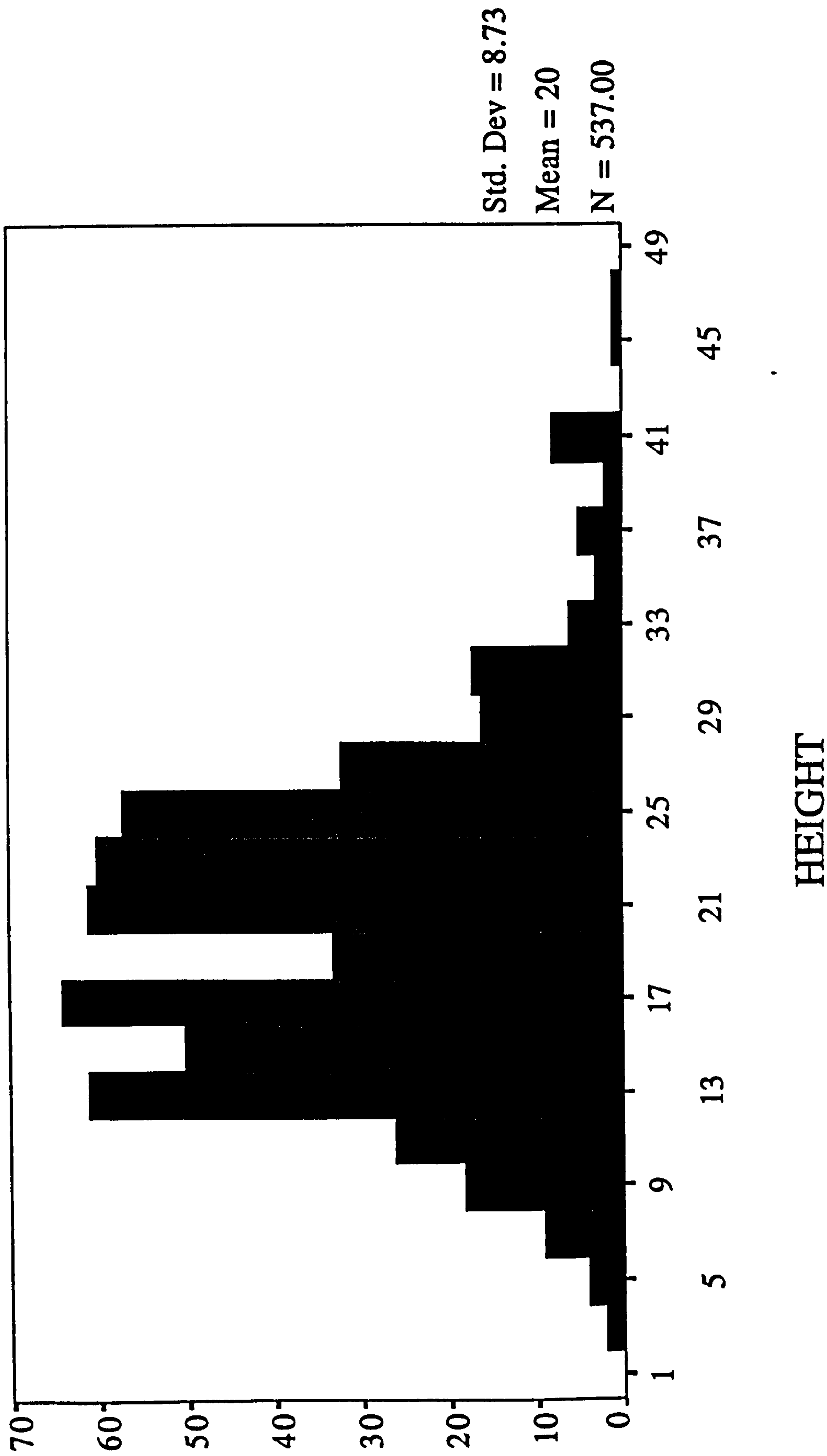
This appendix illustrates histograms, to show the normal distribution of data. Each of the four measured parameters (Length, Height, Hinge Length and Anterior Length), for both species of bivalve (*M. braamburiensis* and *M. morrisi*), at both Calvert and Saxon pits are shown. Histograms of the four measured parameters for *M. braamburiensis* are also shown for Orton pit.

Due to constraints with the package producing the histograms (SPSS), the x axis label can only contain one word. Therefore on the Hinge Length and Anterior Length histograms, the x axis label has the two words joined together. Also the heading on each histogram only shows the first part of each species name: *Meleagrinella* for *M. braamburiensis* and *Mesosacella* for *M. morrisi*.

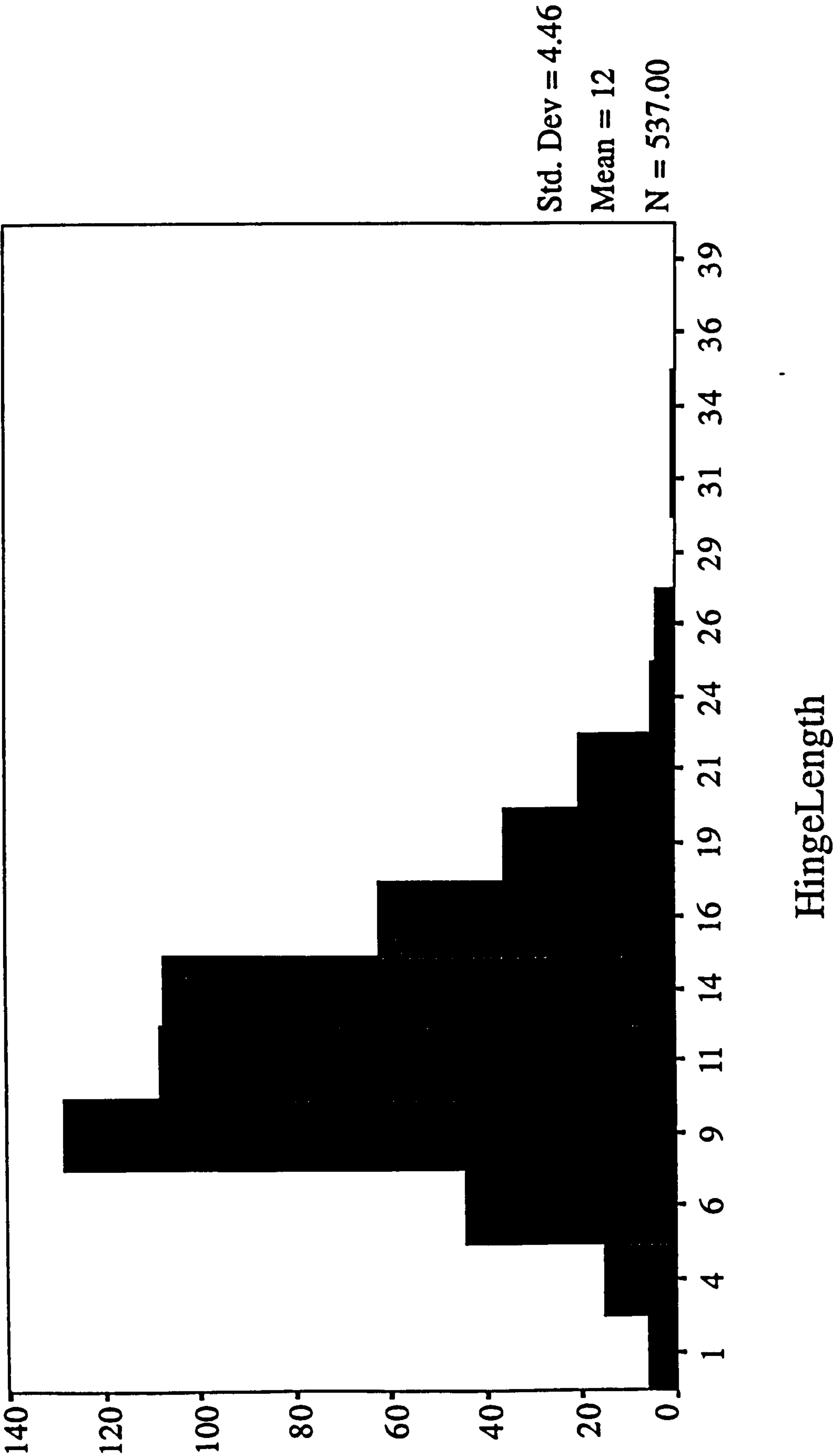
Length Histogram for Meleagrinella, Calvert Pit



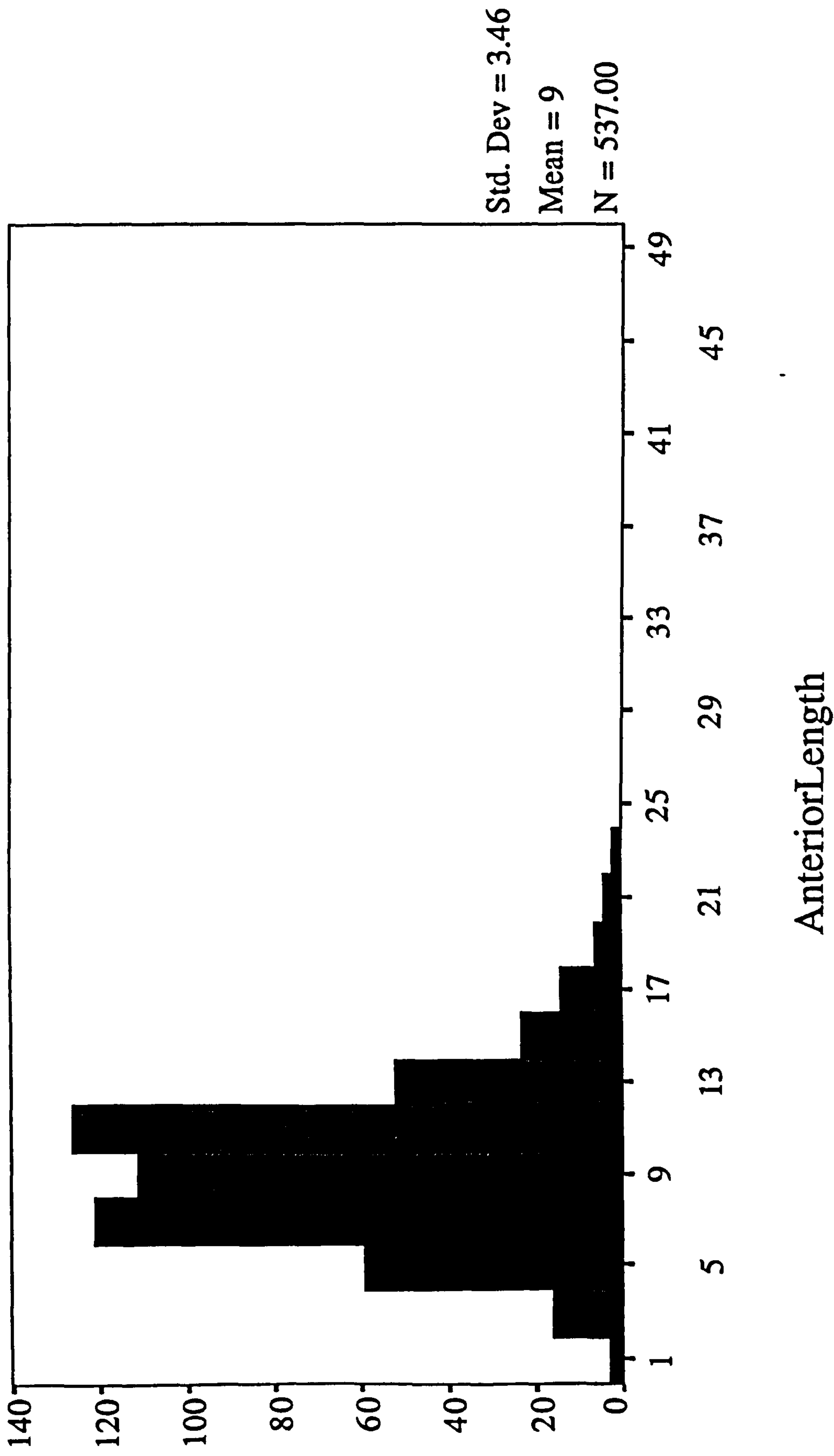
Height Histogram for Meleagrinnella, Calvert Pit



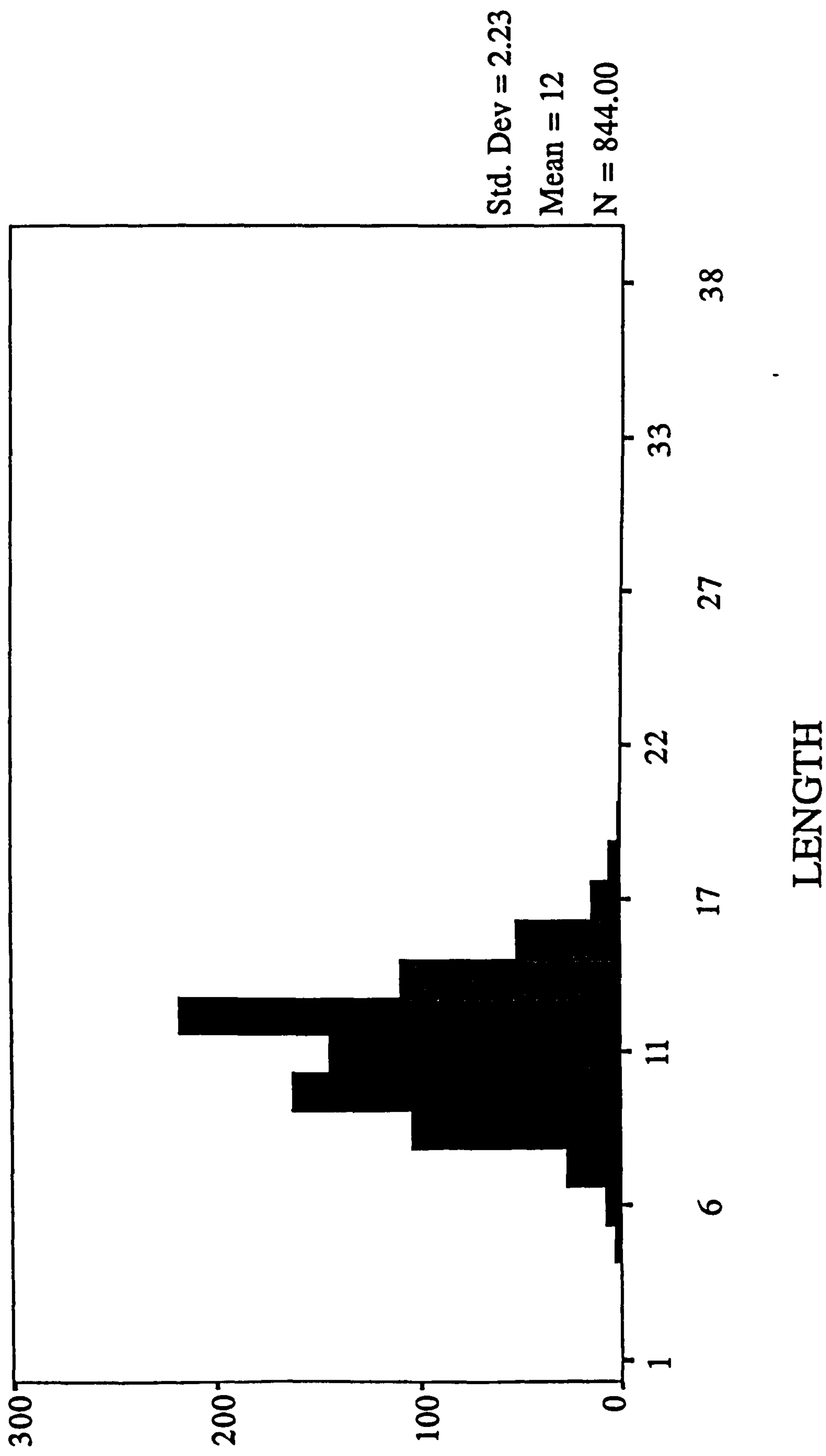
Hinge Length Histogram for Meleagrinella, Calvert Pit



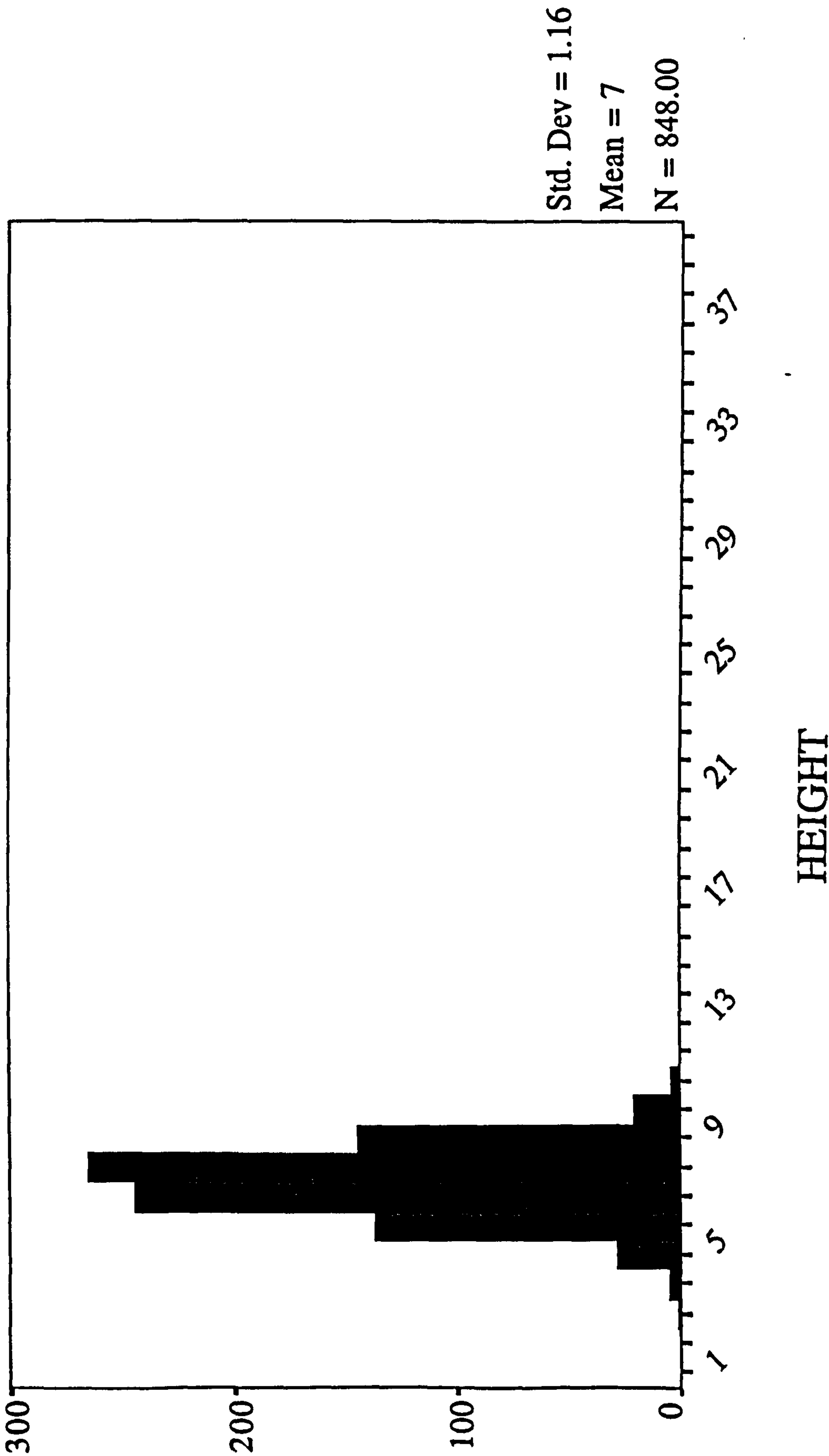
Anterior Length Histogram for Meleagrinnella, Calvert Pit



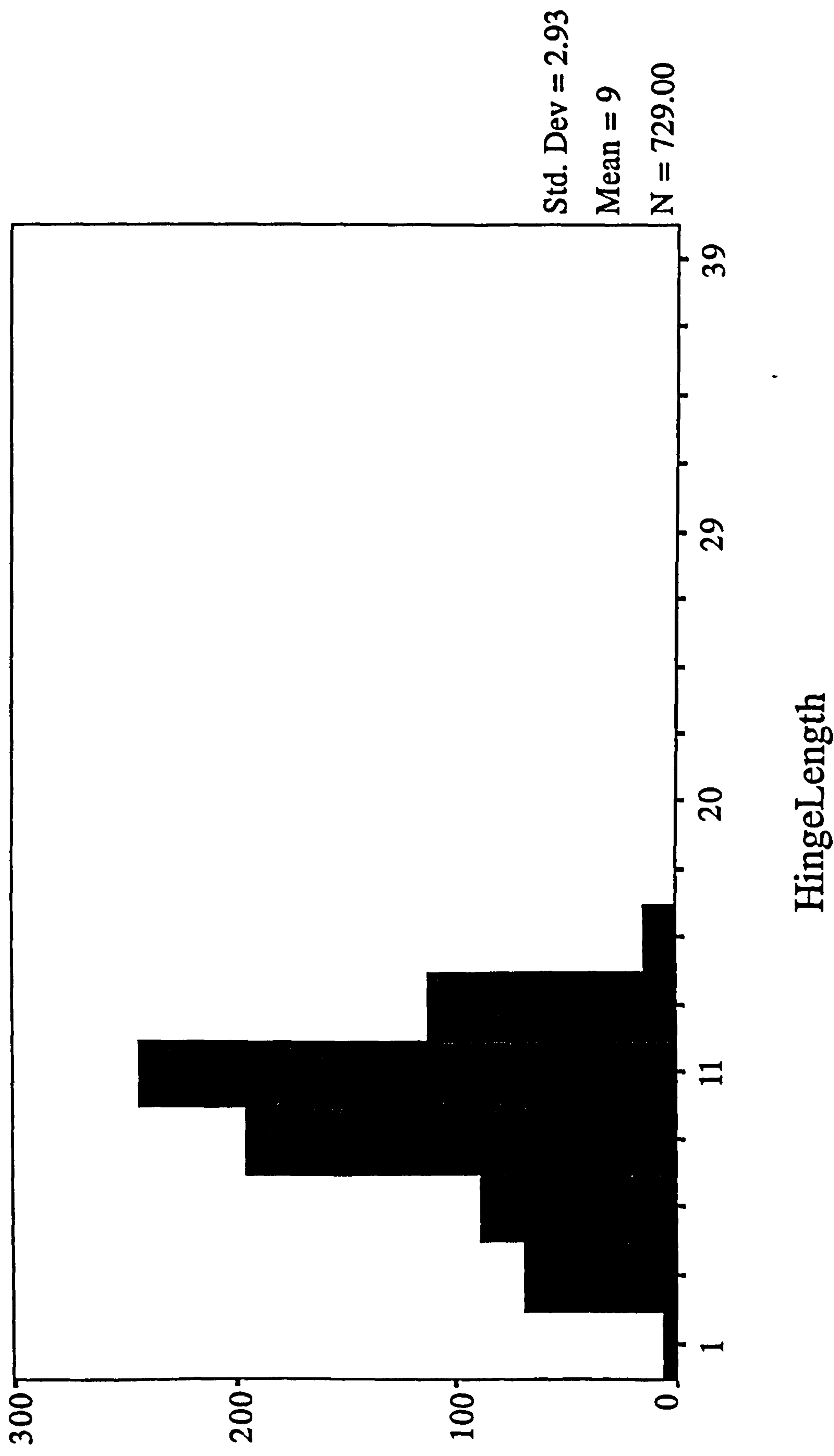
Length for Mesosaccella, Calvert Pit



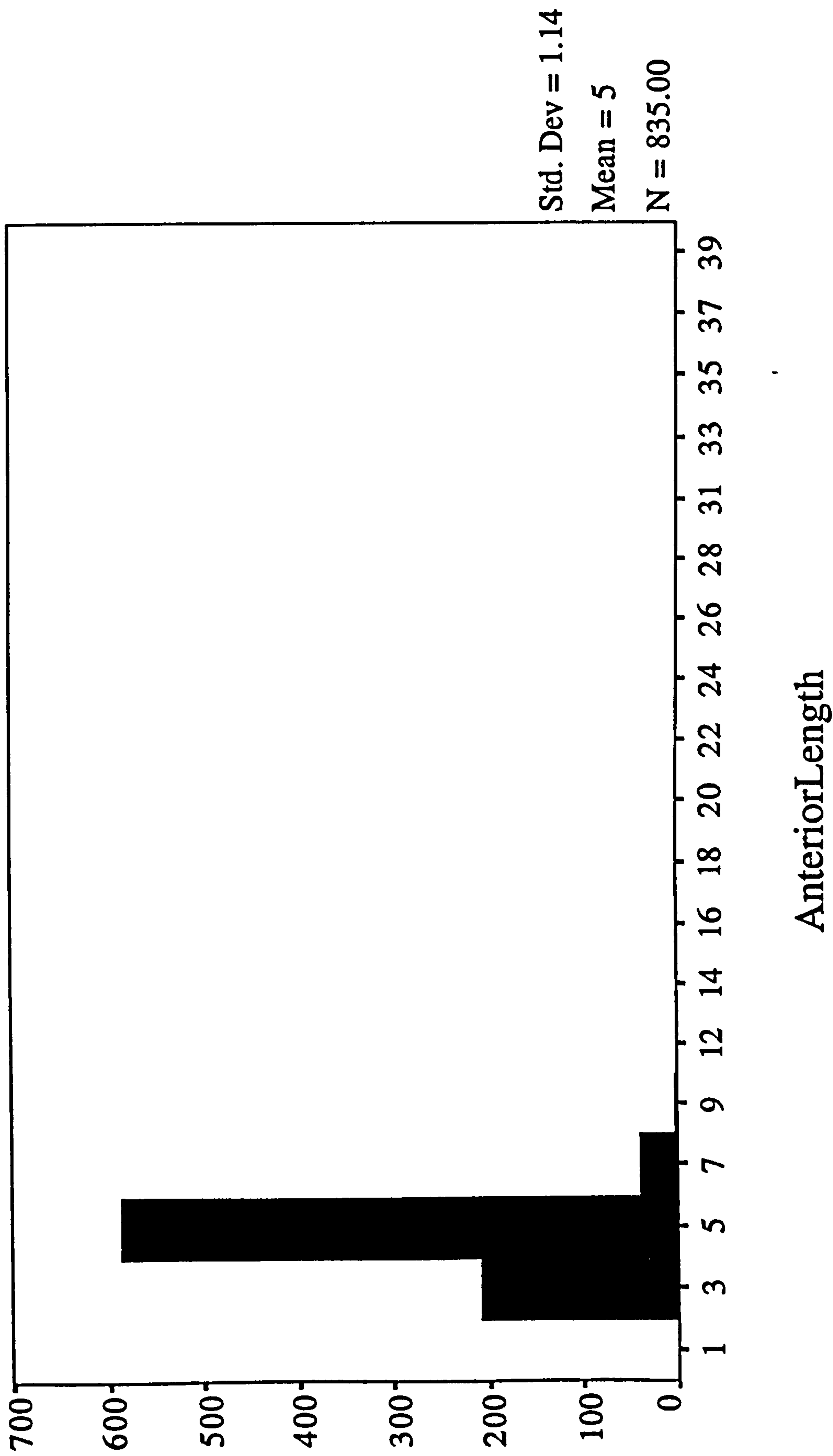
Height for Mesosaccella, Calvert Pit



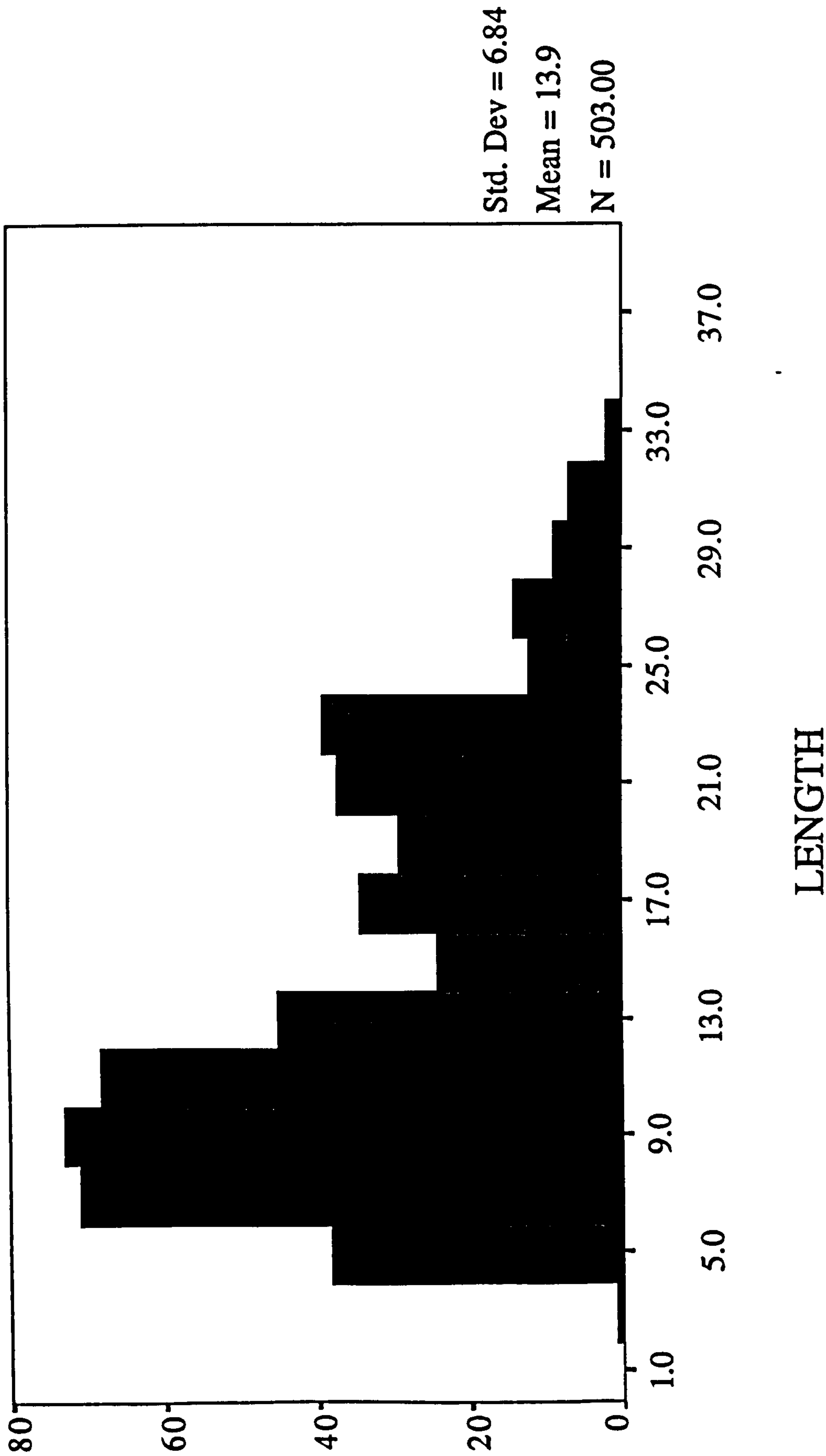
Hinge Length for Mesosaccella, Calvert Pit



Anterior Length for Mesosaccella, Calvert Pit

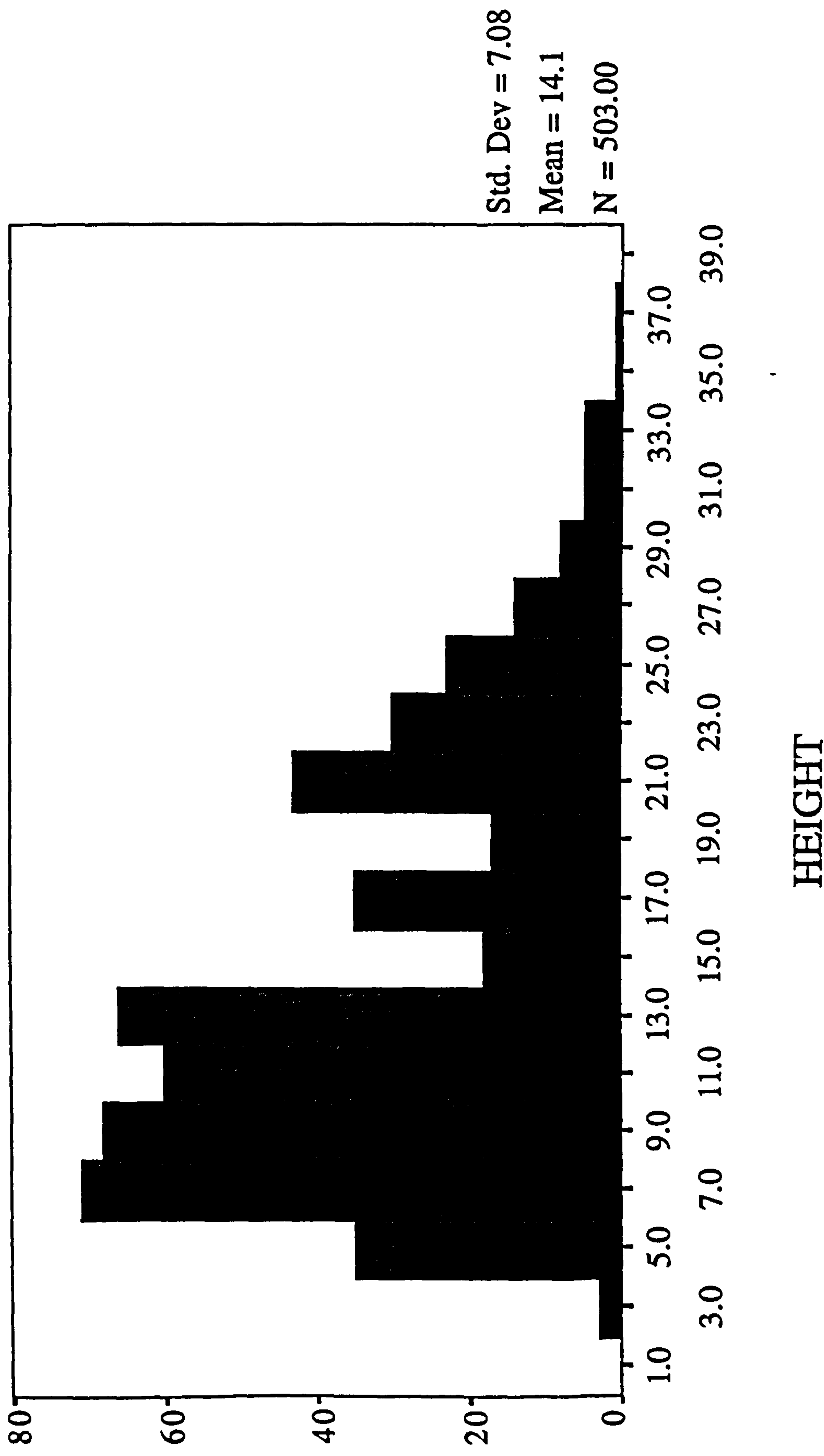


Length Histogram for Meleagrinnella, Saxon Pit

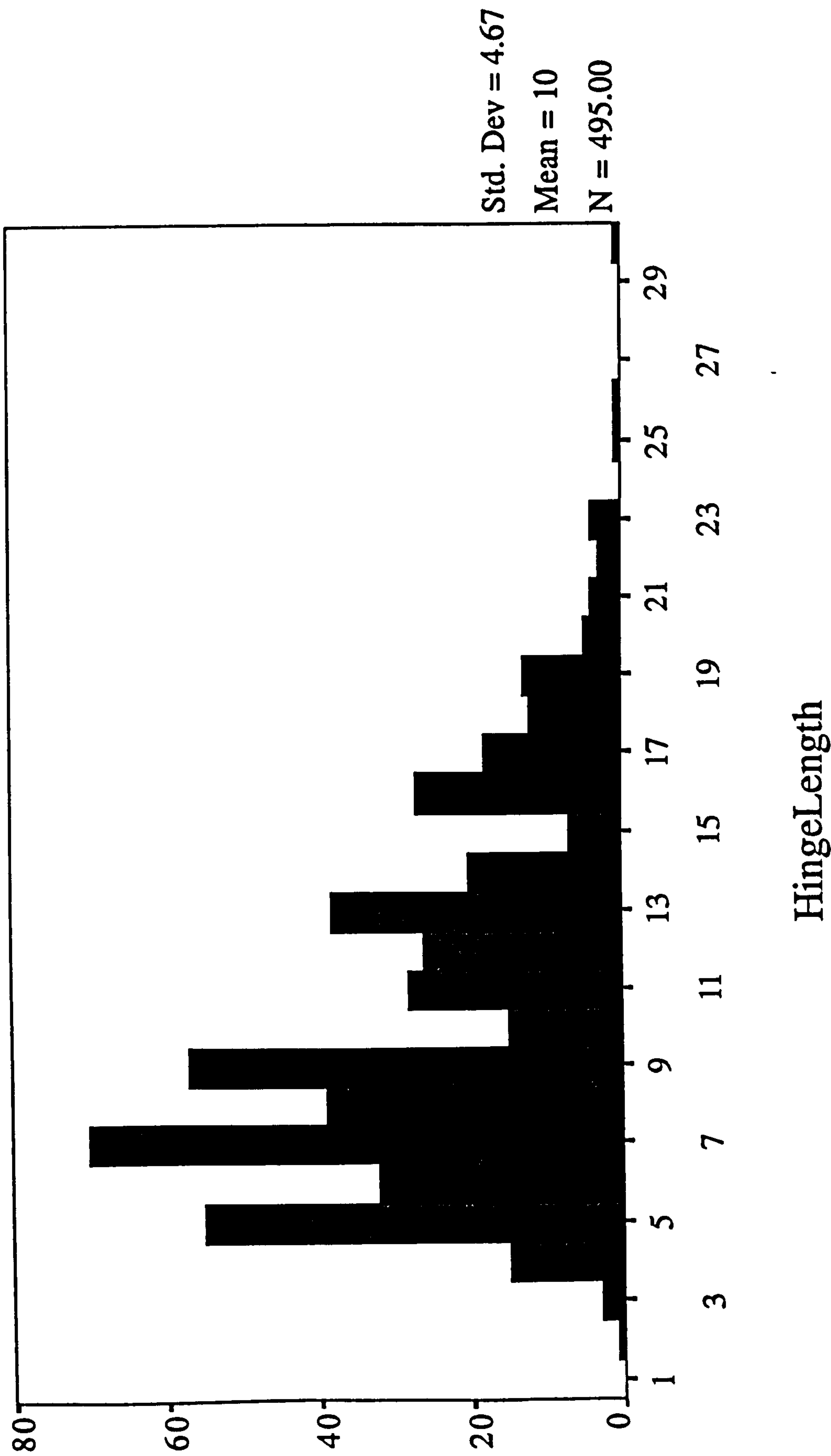


*

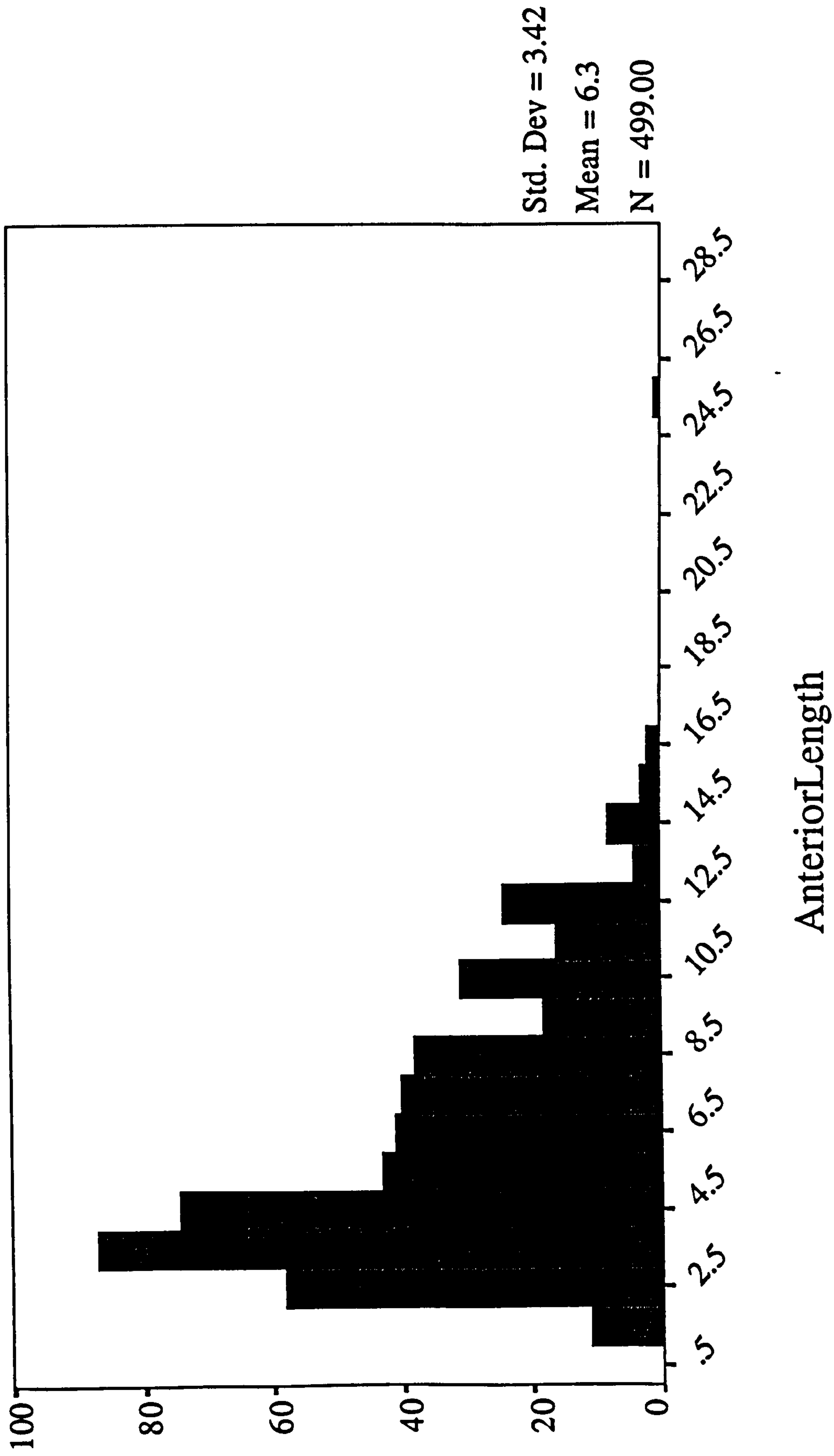
Height Histogram for Meleagrinella, Saxon Pit



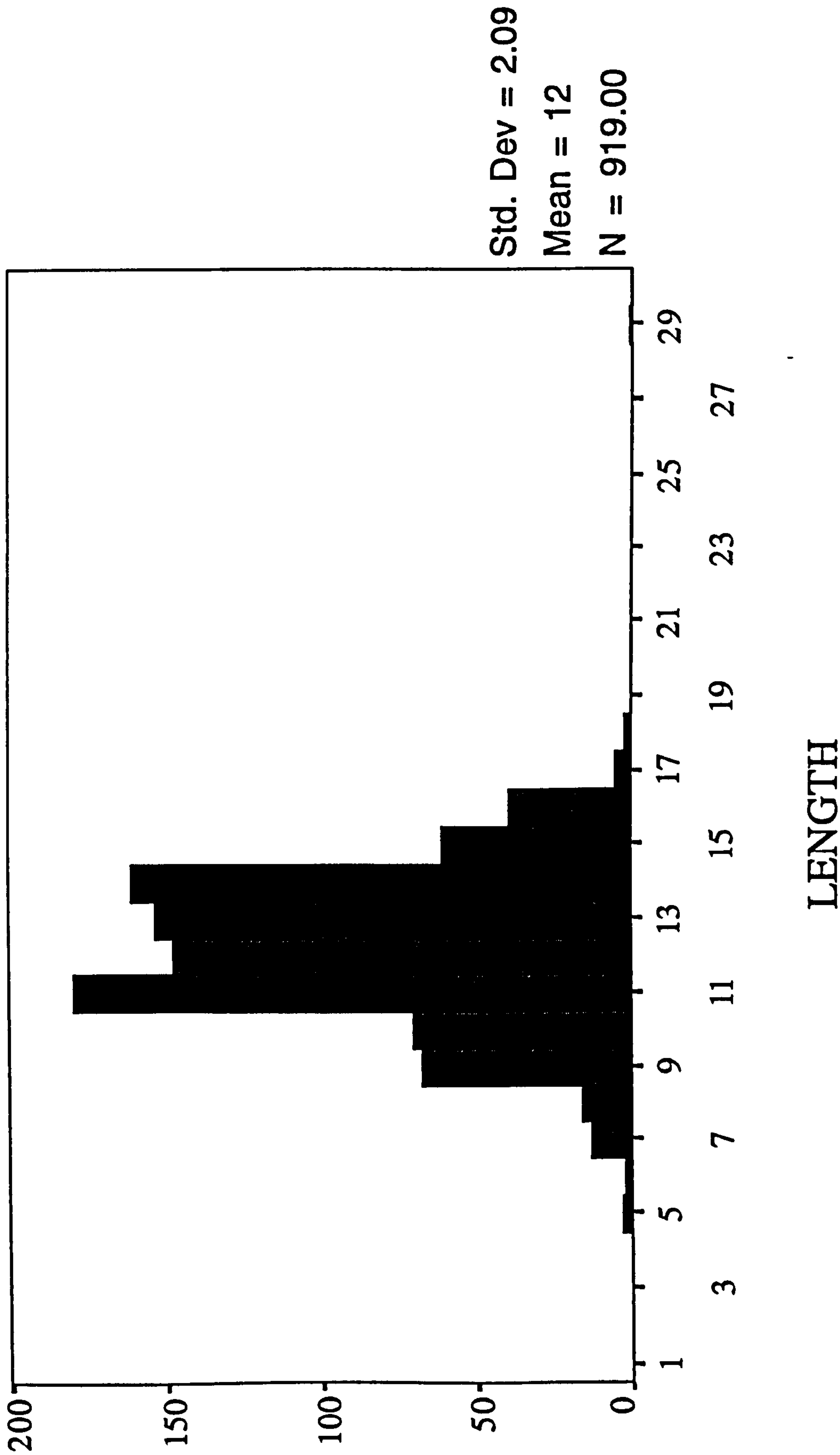
Hinge Length Histogram for Meleagrinella, Saxon Pit



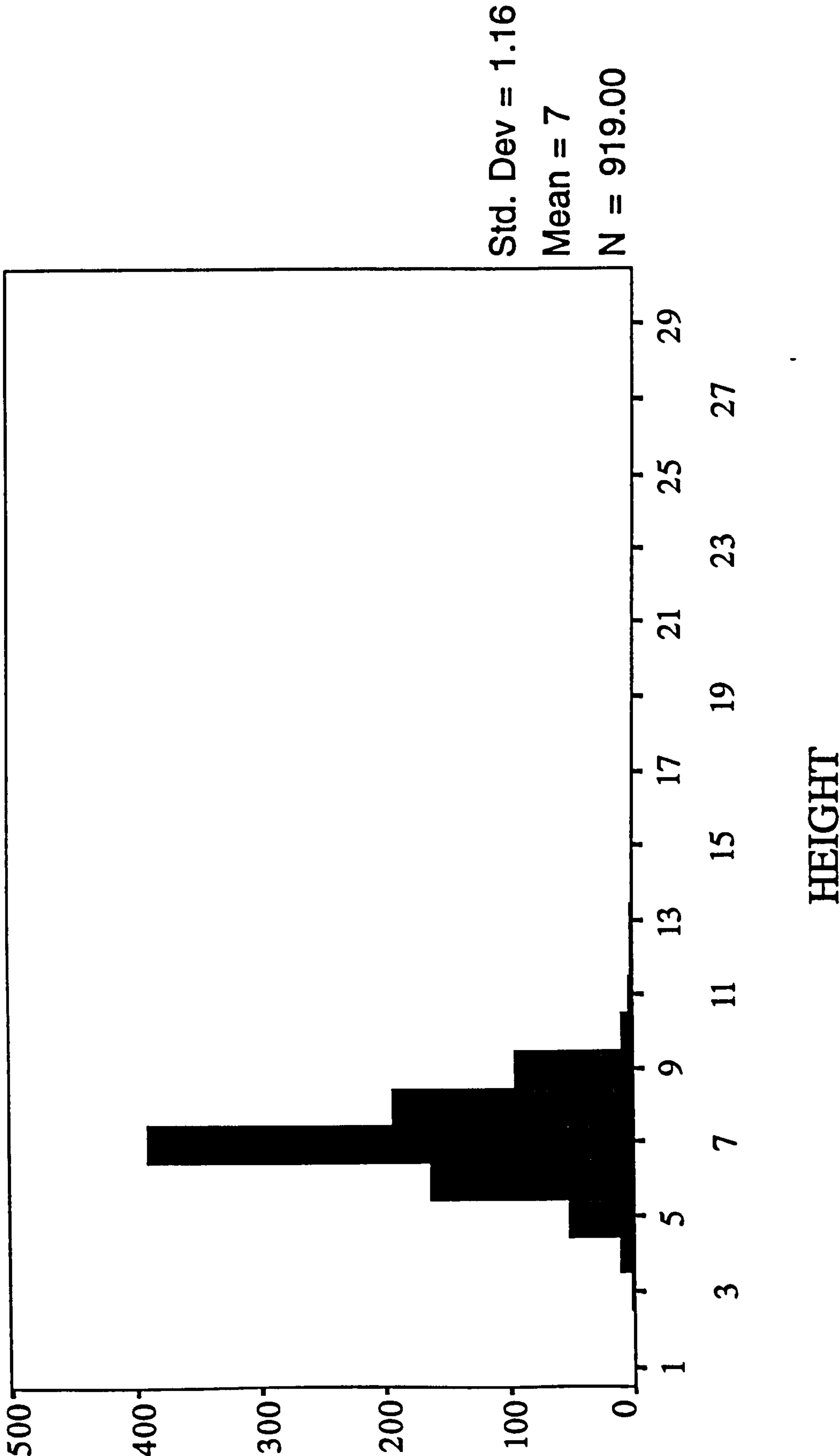
Anterior Length Histogram for Meleagrinella, Saxon Pit



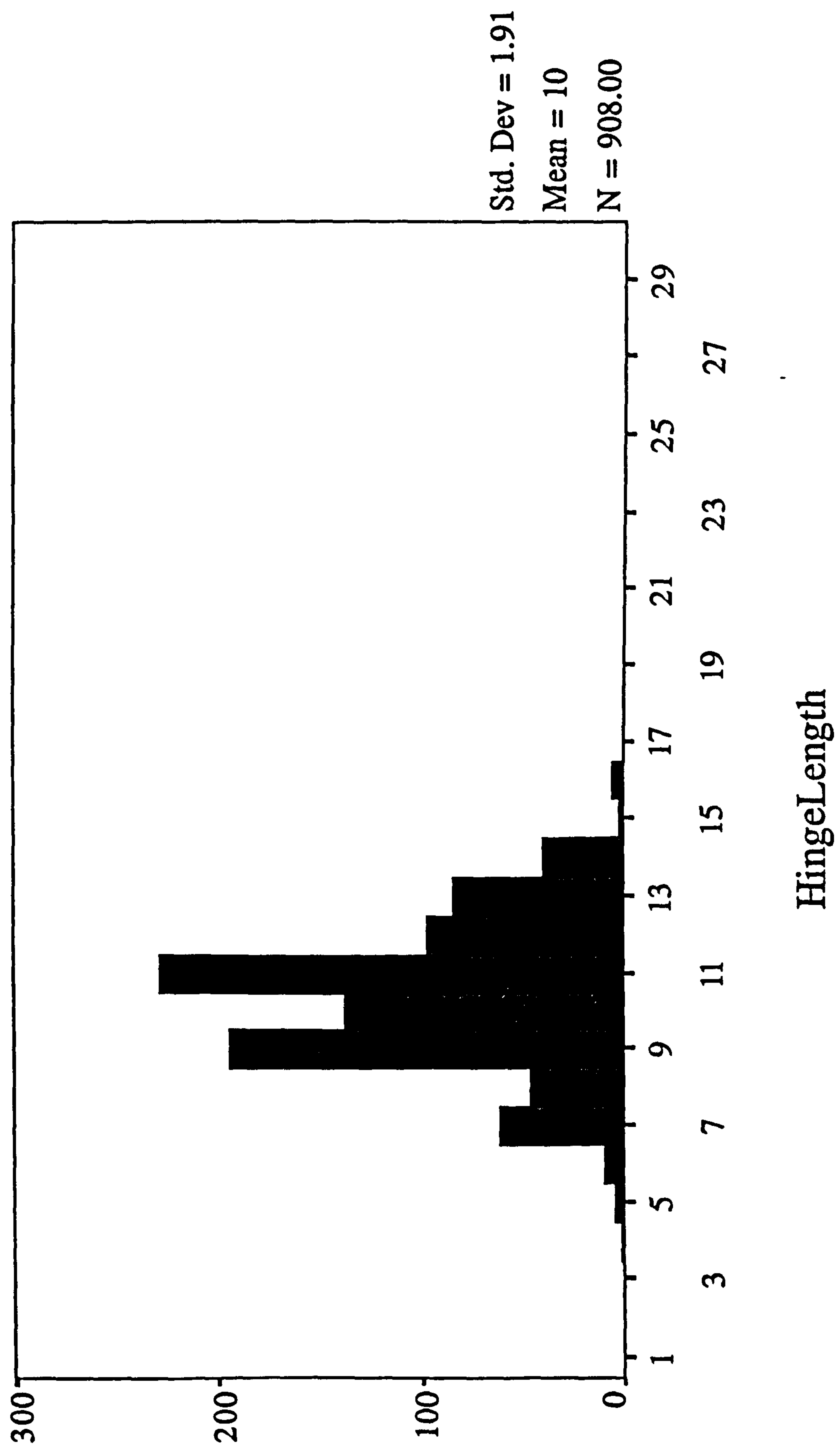
Length Histogram for Mesosaccella, Saxon Pit



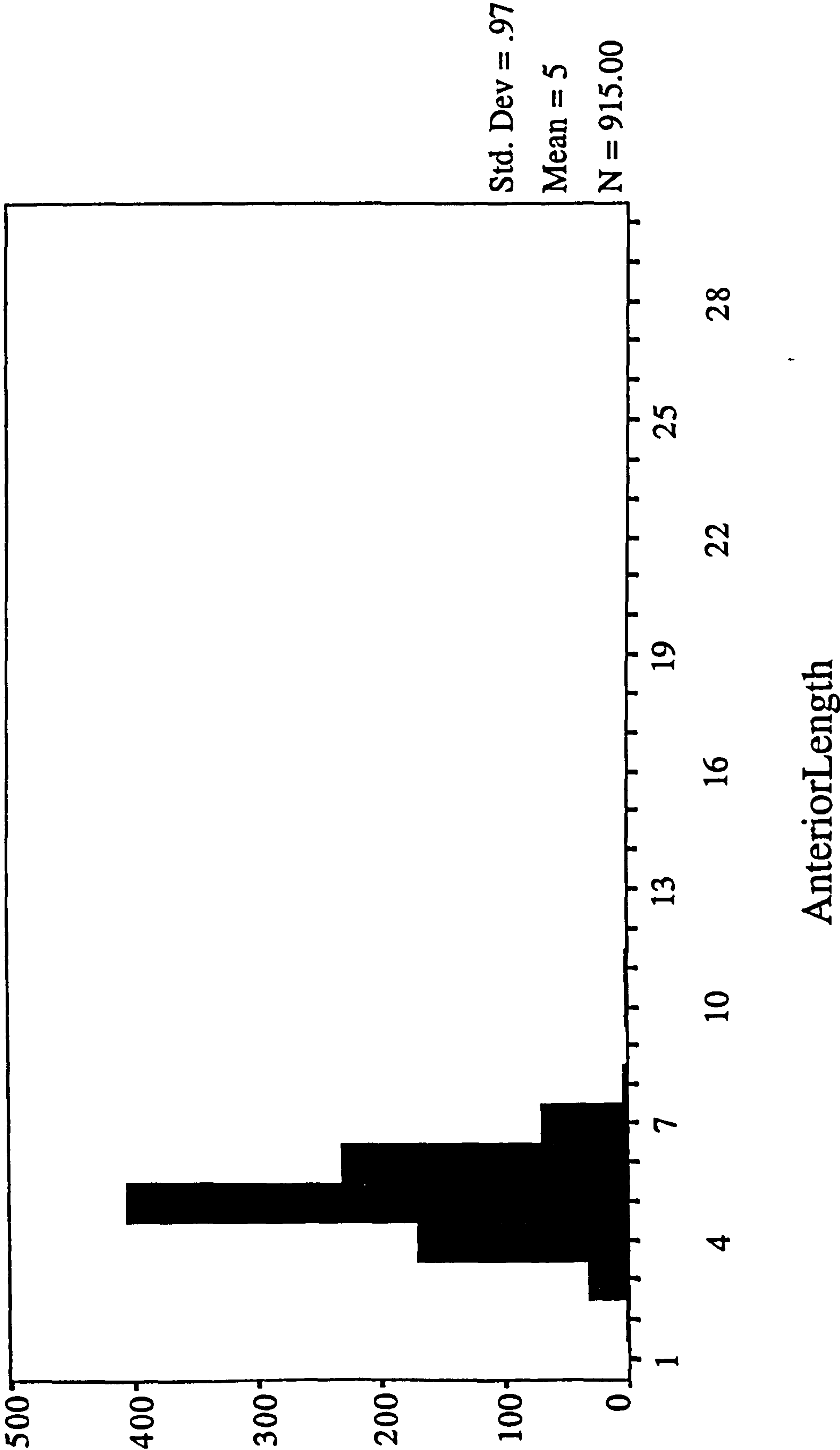
Height Histogram for Mesosaccella, Saxon Pit



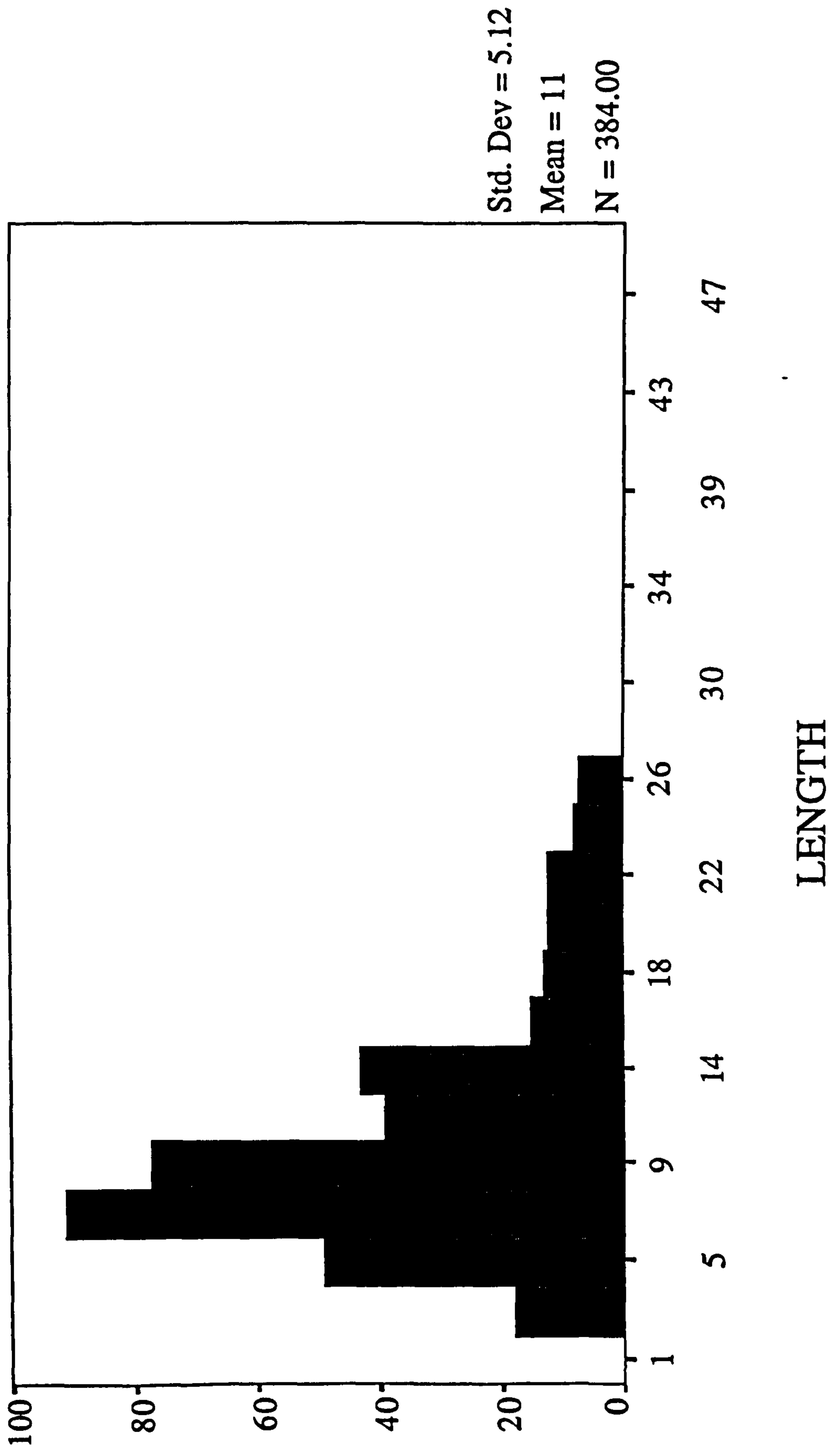
Hinge Length Histogram for Mesosaccella, Saxon Pit



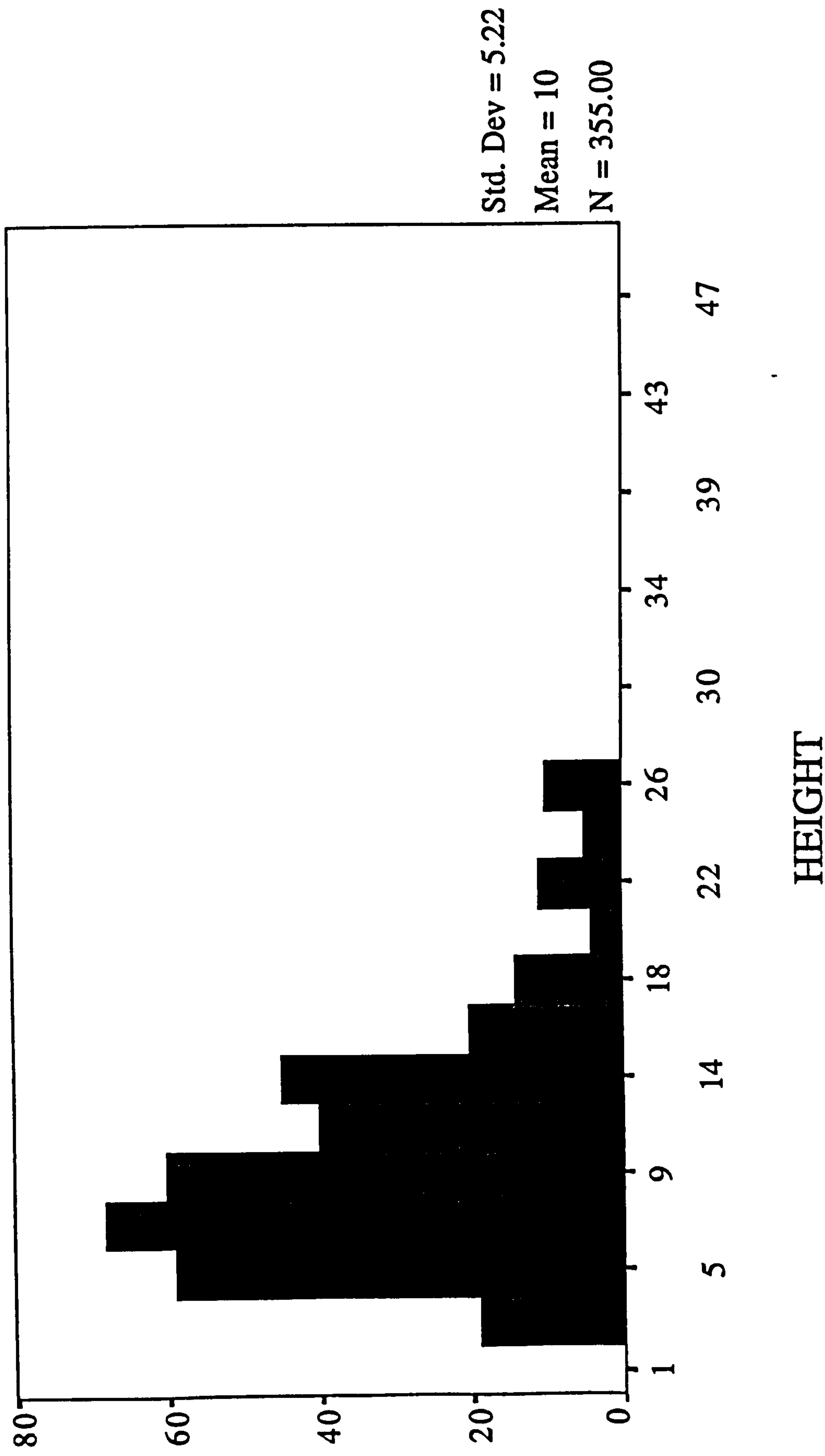
Anterior Length Histogram for Mesosaccella, Saxon Pit



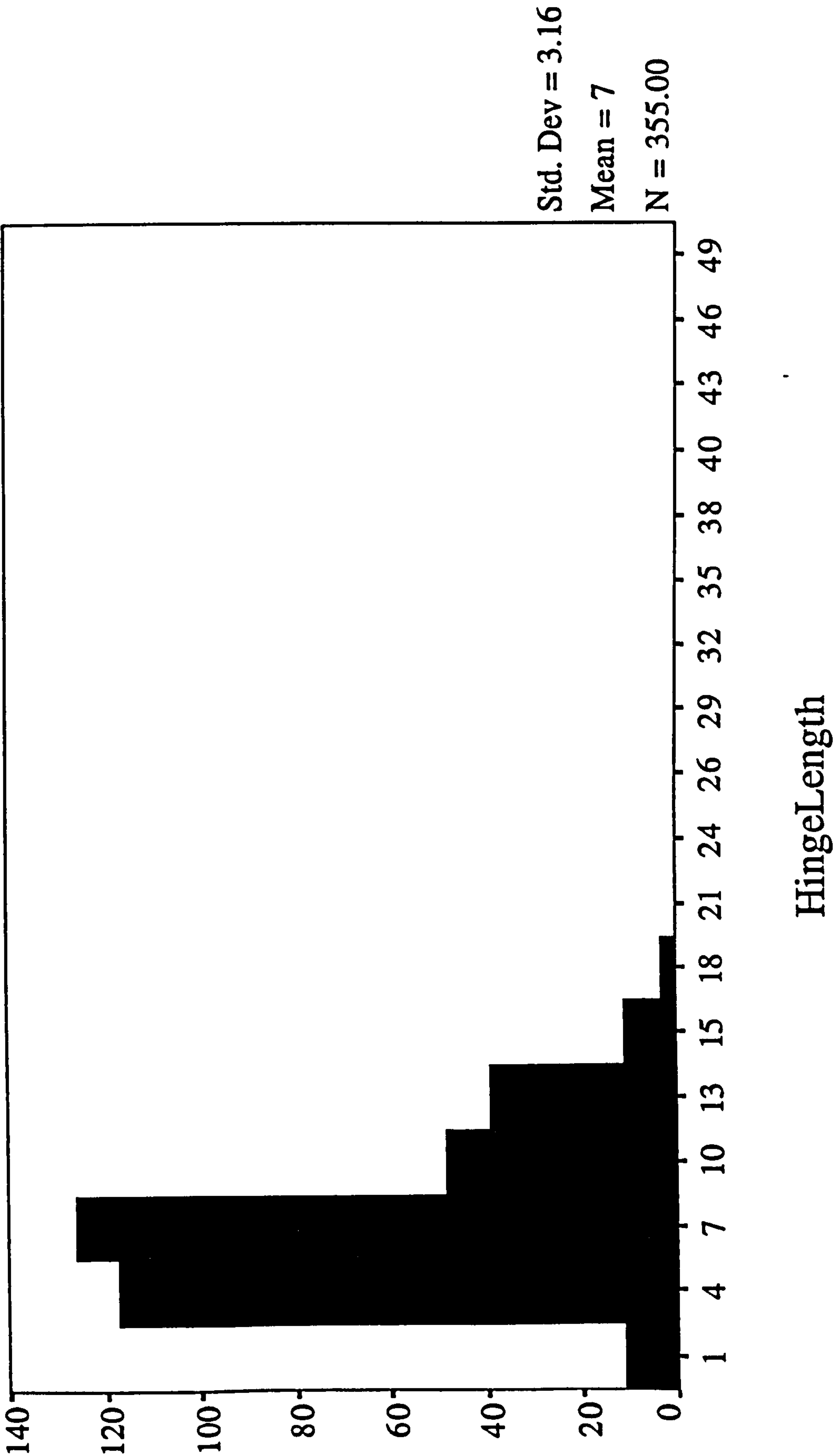
Length Histogram for Meleagrinella, Orton Pit



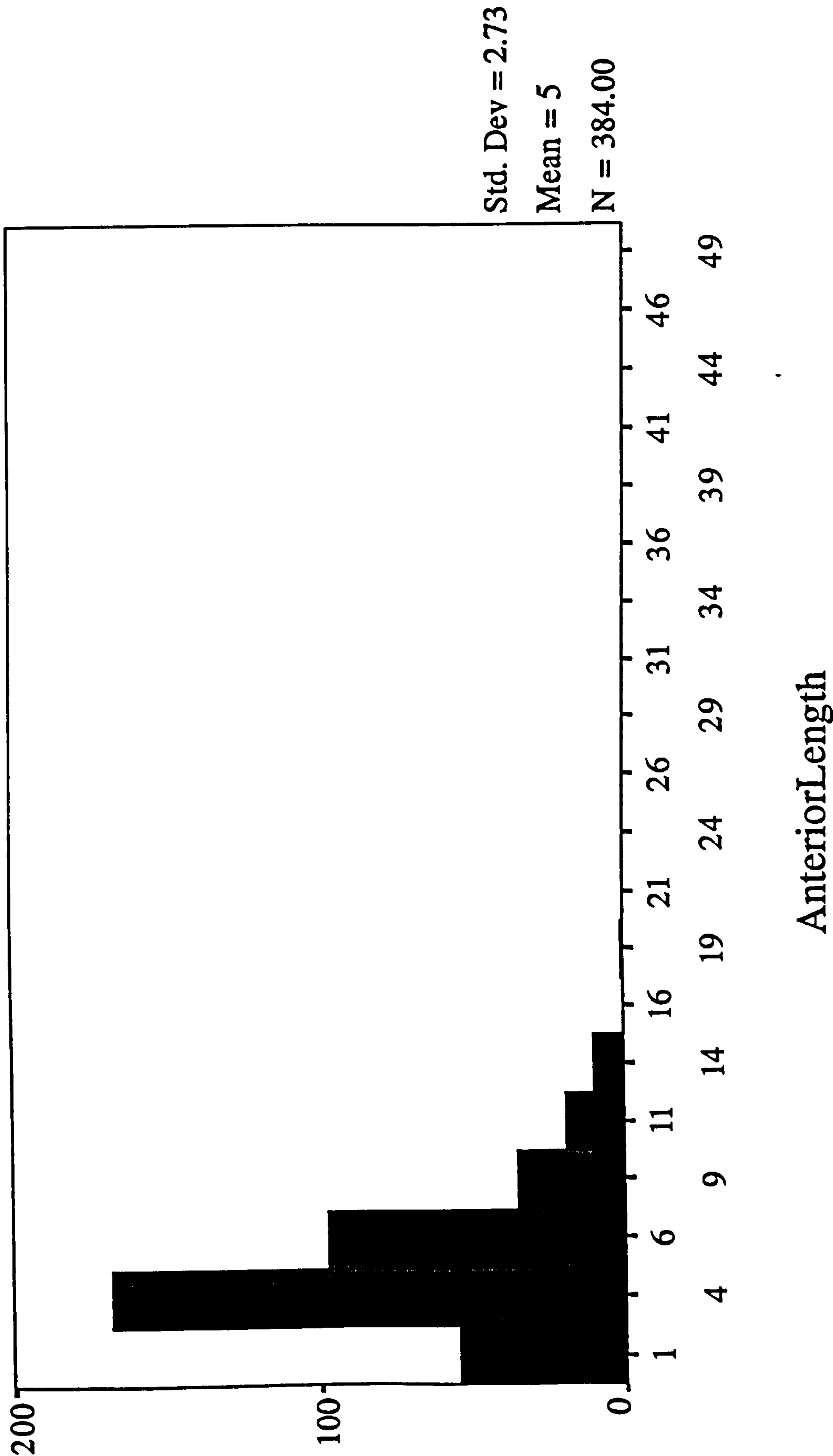
Height Histogram for Meleagrinnella, Orton Pit



Hinge Length Histogram for Meleagrinella, Orton Pit



Anterior Length Histogram for Meleagrinella, Orton Pit



APPENDIX FOUR

This appendix contains a copy of the paper by Macquaker & Howell, which is currently in press with The Journal of the Geological Society, London.

It also contains Figures and all colour plates used in conjunction with this paper entitled A4 within the main text. Table A4.1 gives semi-quantitative descriptions of all samples.

Table 1 Datum top of Bed 14 (of Hudson and Martill, 1994)										
Real Depth	Facies	Detrital			Nannoplankton	Authigenic Carbonate	Macro-shell debris	Authigenic		Visible organic matter
		Sand	Silt	Clay				Pyrite	Clay	
Saxon Pit -3.15	Silt-rich mudstone	0.0%	5.0%	91.5%	0.5%	0.0%	1.0%	1.0%	0.0%	1.0%
Saxon Pit -3.0	Silt-rich mudstone	0.0%	7.5%	89.5%	1.0%	0.0%	0.5%	0.5%	0.0%	1.0%
Saxon Pit -2.85	Clay-rich mudstone	0.0%	4.0%	93.0%	1.0%	0.0%	0.5%	0.5%	0.0%	1.0%
Saxon Pit -2.7	Silt-rich mudstone	0.0%	5.0%	91.5%	1.0%	0.0%	1.0%	0.5%	0.0%	1.0%
Saxon Pit -2.55	Clay-rich mudstone	0.0%	4.0%	91.5%	2.5%	0.0%	0.5%	0.5%	0.0%	1.0%
Saxon Pit -2.4	Clay-rich mudstone	0.0%	4.0%	93.0%	1.0%	0.0%	0.5%	0.5%	0.0%	1.0%
Saxon Pit -2.25	Silt-rich mudstone	0.0%	5.0%	84.5%	2.5%	1.0%	5.0%	1.0%	0.0%	1.0%
Saxon Pit -2.1	Silt-rich mudstone	0.0%	7.5%	89.5%	0.5%	0.0%	0.5%	1.0%	0.0%	1.0%
Saxon Pit -1.95	Silt-rich mudstone	0.0%	8.0%	89.0%	0.5%	0.0%	1.0%	0.5%	0.0%	1.0%
Saxon Pit -1.8	Clay-rich mudstone	0.0%	4.0%	93.5%	0.5%	0.0%	0.5%	0.5%	0.0%	1.0%
Saxon Pit -1.65	Silt-rich mudstone	0.0%	5.0%	87.5%	1.0%	0.0%	5.0%	0.5%	0.0%	1.0%
Saxon Pit -1.5	Silt-rich mudstone	0.0%	5.0%	92.0%	0.5%	0.0%	0.5%	1.0%	0.0%	1.0%
Saxon Pit -1.35	Silt-rich mudstone	0.0%	7.5%	90.0%	0.5%	0.0%	0.5%	0.5%	0.0%	1.0%
Saxon Pit -1.1	Clay-rich mudstone	0.0%	4.0%	92.0%	0.5%	0.0%	1.0%	0.5%	0.0%	2.0%
Saxon Pit -1.05	Clay-rich mudstone	0.0%	4.0%	93.0%	0.5%	0.0%	1.0%	0.5%	0.0%	1.0%
Saxon Pit -0.9	Silt-rich mudstone	0.0%	5.0%	89.0%	0.5%	0.0%	2.5%	2.0%	0.0%	1.0%
Saxon Pit -0.75	Silt-rich mudstone	0.0%	7.5%	88.5%	0.5%	0.5%	1.0%	1.0%	0.0%	1.0%
Saxon Pit -0.6	Silt-rich mudstone	0.0%	10.0%	85.5%	0.5%	0.5%	0.0%	1.0%	0.5%	2.0%
Saxon Pit -0.45	Clay-rich mudstone	0.0%	4.0%	83.5%	0.5%	2.0%	8.0%	1.0%	0.0%	1.0%
Saxon Pit -0.3	Silt-rich mudstone	0.0%	7.5%	84.5%	0.5%	0.5%	5.0%	1.0%	0.0%	1.0%
Saxon Pit -0.15	Silt-rich mudstone	0.0%	9.0%	86.0%	1.0%	0.0%	2.0%	1.0%	0.0%	1.0%
Saxon Pit 0.07	Silt-rich mudstone	0.0%	15.0%	68.0%	0.5%	5.0%	10.0%	0.5%	0.0%	1.0%
Saxon Pit 0.21	Silt-rich mudstone	0.0%	10.0%	77.0%	1.0%	2.5%	7.5%	1.0%	0.0%	1.0%
Saxon Pit 0.33	Silt-rich mudstone	0.0%	12.5%	70.0%	0.5%	0.5%	15.0%	0.5%	0.0%	1.0%
Saxon Pit 0.53	Clay-rich mudstone	0.0%	2.5%	93.5%	1.0%	0.0%	1.0%	1.0%	0.0%	1.0%
Saxon Pit 0.68	Silt-rich mudstone	0.0%	6.0%	91.5%	0.5%	0.0%	0.5%	0.5%	0.0%	1.0%
Saxon Pit 0.83	Clay-rich mudstone	0.0%	4.0%	91.0%	0.5%	0.0%	2.5%	1.0%	0.0%	1.0%
Saxon Pit 0.98	Clay-rich mudstone	0.0%	4.0%	93.5%	0.5%	0.0%	0.0%	1.0%	0.0%	1.0%
Saxon Pit 1.13	Clay-rich mudstone	0.0%	2.5%	90.5%	0.0%	0.0%	5.0%	1.0%	0.0%	1.0%
Saxon Pit 1.28	Silt-rich mudstone	0.0%	5.0%	92.5%	0.5%	0.0%	0.0%	1.0%	0.0%	1.0%
Saxon Pit 1.43	Silt-rich mudstone	0.0%	7.5%	90.0%	0.5%	0.0%	0.0%	1.0%	0.0%	1.0%
Saxon Pit 1 -3.0	Silt-rich mudstone	0.0%	7.5%	90.0%	0.5%	0.0%	0.5%	0.5%	0.0%	1.0%
Saxon Pit 2 -3.0	Silt-rich mudstone	0.0%	7.5%	90.0%	0.5%	0.0%	0.5%	0.5%	0.0%	1.0%
Saxon Pit 3 -3.0	Silt-rich mudstone	0.0%	7.5%	89.5%	1.0%	0.0%	0.5%	0.5%	0.0%	1.0%
Saxon Pit 4 -3.0	Silt-rich mudstone	0.0%	7.5%	89.5%	1.0%	0.0%	0.5%	0.5%	0.0%	1.0%
Saxon Pit 5 -3.0	Silt-rich mudstone	0.0%	7.5%	89.5%	1.0%	0.0%	0.5%	0.5%	0.0%	1.0%
Saxon Pit 6 -3.0	Silt-rich mudstone	0.0%	10.0%	87.0%	1.0%	0.0%	0.5%	0.5%	0.0%	1.0%
Saxon Pit 7 -3.0	Silt-rich mudstone	0.0%	10.0%	87.0%	1.0%	0.0%	0.5%	0.5%	0.0%	1.0%
Saxon Pit 8 -3.0	Silt-rich mudstone	0.0%	5.0%	92.0%	1.0%	0.0%	0.5%	0.5%	0.0%	1.0%
Saxon Pit 9 -3.0	Silt-rich mudstone	0.0%	7.5%	89.0%	1.0%	0.0%	1.0%	0.5%	0.0%	1.0%
Saxon Pit 10 -3.0	Silt-rich mudstone	0.0%	7.5%	89.5%	1.0%	0.0%	0.5%	0.5%	0.0%	1.0%
Saxon Pit 11 -3.0	Silt-rich mudstone	0.0%	7.5%	89.5%	1.0%	0.0%	0.5%	0.5%	0.0%	1.0%
Saxon Pit 12 -3.0	Silt-rich mudstone	0.0%	7.5%	89.0%	1.0%	0.0%	1.0%	0.5%	0.0%	1.0%
Saxon Pit 13 -3.0	Silt-rich mudstone	0.0%	5.0%	91.5%	1.0%	0.0%	1.0%	0.5%	0.0%	1.0%
Saxon Pit 14 -3.0	Clay-rich mudstone	0.0%	2.5%	94.0%	1.0%	0.0%	1.0%	0.5%	0.0%	1.0%
Saxon Pit 15 -3.0	Silt-rich mudstone	0.0%	7.5%	89.0%	1.0%	0.0%	1.0%	0.5%	0.0%	1.0%
Kings Dyke 1 -3.0	Silt-rich mudstone	0.0%	10.0%	86.5%	1.0%	0.0%	1.0%	0.5%	0.0%	1.0%
Kings Dyke 2 -3.0	Silt-rich mudstone	0.0%	10.0%	86.5%	1.0%	0.0%	1.0%	0.5%	0.0%	1.0%
Kings Dyke 3 -3.0	Silt-rich mudstone	0.0%	10.0%	86.5%	1.0%	0.0%	1.0%	0.5%	0.0%	1.0%

TABLE A4.1

PLATE A4.1

The studied section at Saxon pit, Peterborough (grid reference TL 248 965). Arrow numbered 1 points to top of bed 14. Arrow numbered 2 points to bed 18. The other arrows point to beds 15, 16 and 17. Bed 14 and 18 are also numbered.

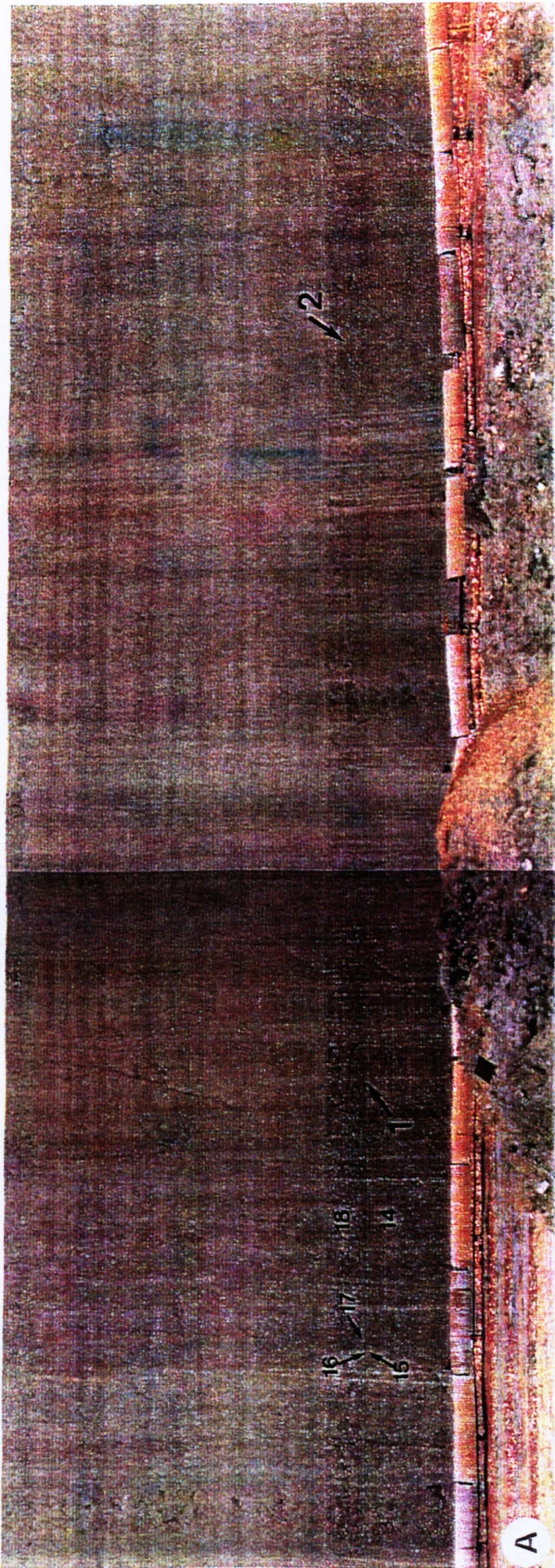


PLATE A4.2

Plate A shows numerous flattened burrows indicating bioturbation. The field of view is 8.9 mm. Plate B shows a remnant upward-fining couplet. The field of view is 2.2 mm. Both samples are from sample location -1.35, Saxon pit (see Figure A4.1).

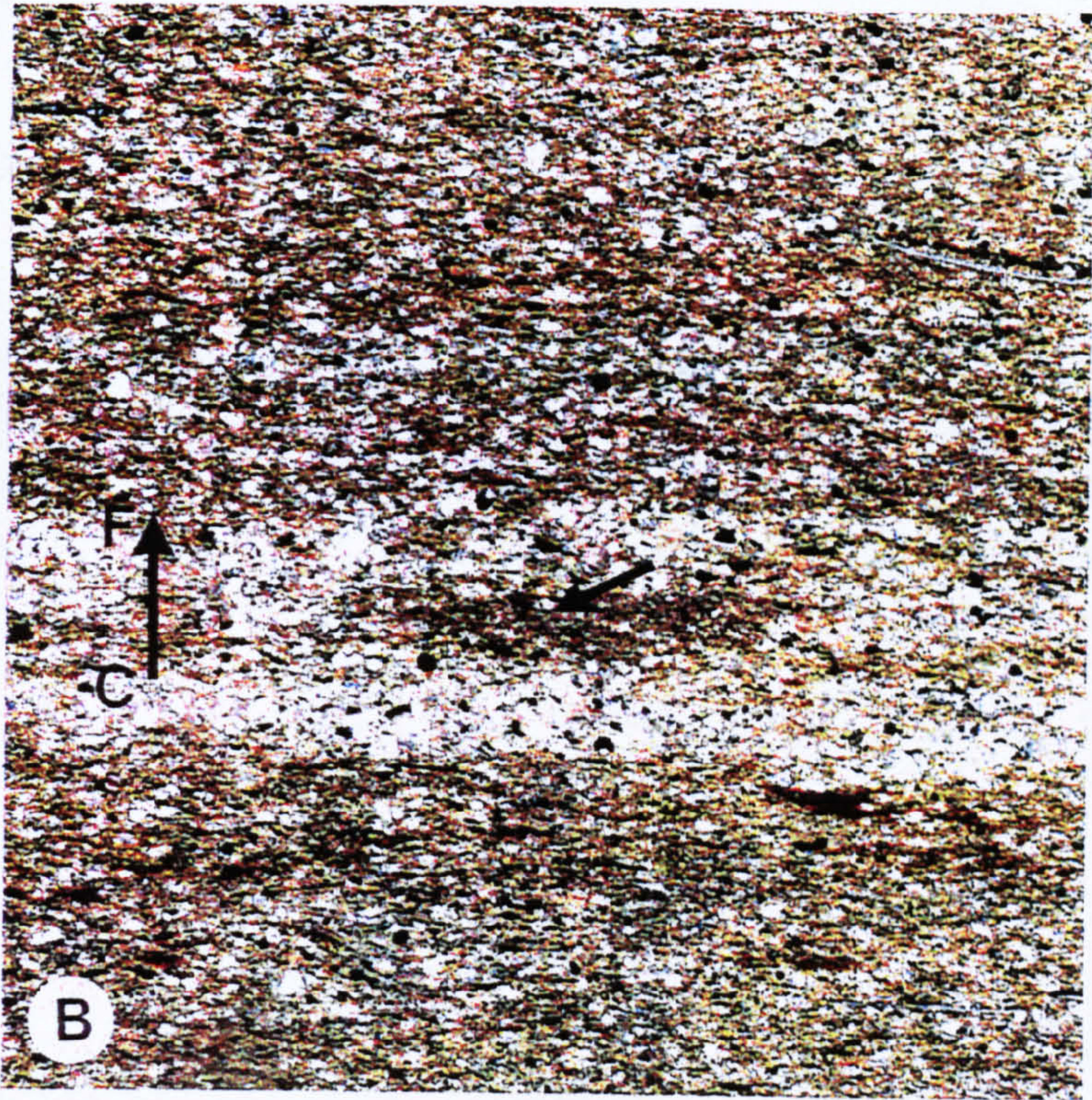
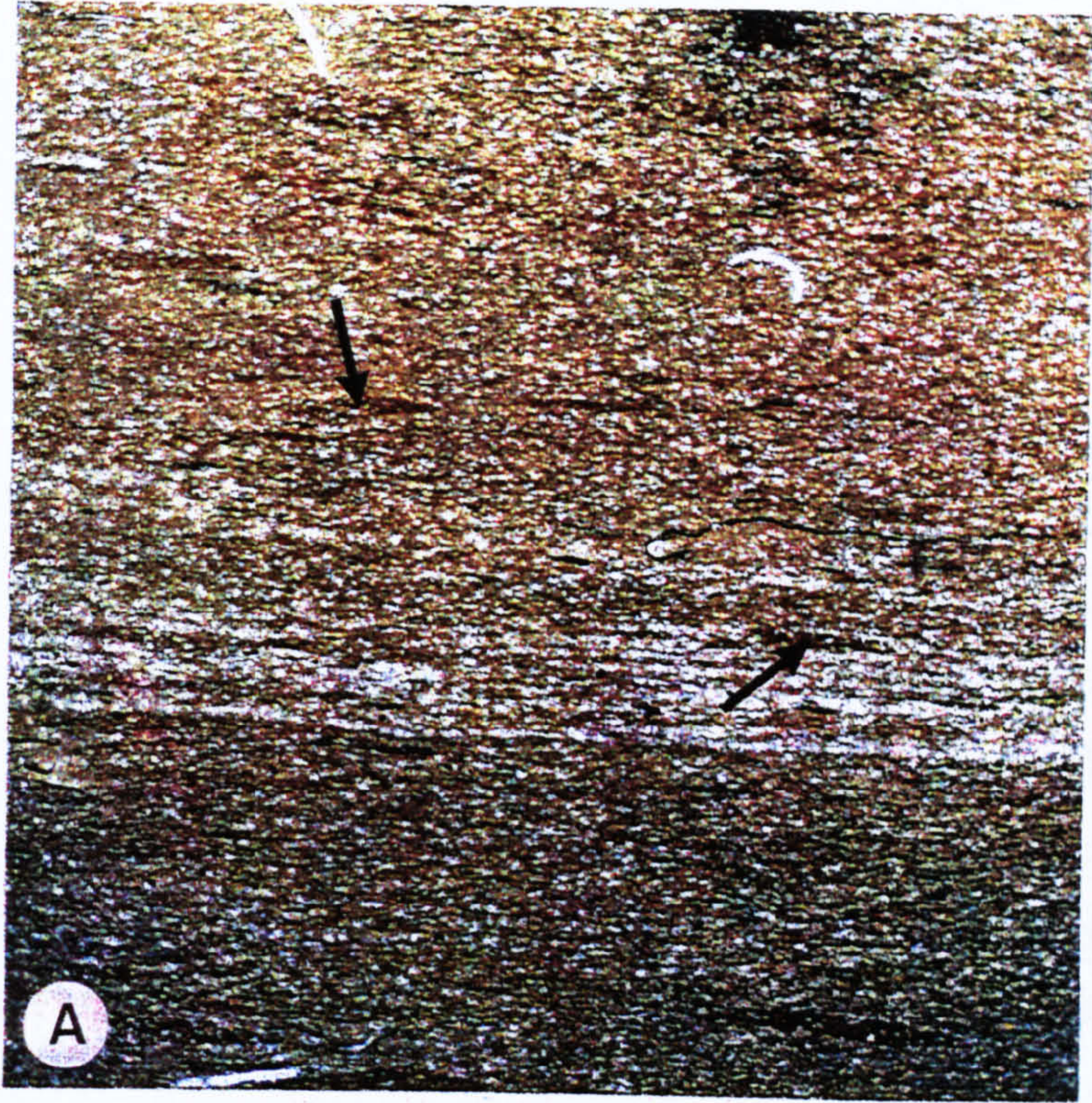


PLATE A4.3

Optical and BSE (backscattered electron) micrographs of vertical samples –3.15 to –2.70, Saxon pit (see Figure A4.1). Descriptions of the samples are given in Table A4.1.

- A optical micrograph of sample –2.70 (scale = x4); a silt-rich mudstone
- B BSE micrograph of sample –2.70 (scale = x250); a silt-rich mudstone
- C optical micrograph of sample –2.85 (scale = x4); a clay-rich mudstone
- D BSE micrograph of sample –2.85 (scale = x250); a clay-rich mudstone
- E optical micrograph of sample –3.0 (scale = x4); a silt-rich mudstone
- F BSE micrograph of sample –3.0 (scale = x250); a silt-rich mudstone
- G optical micrograph of sample –3.15 (scale = x4); a silt-rich mudstone
- H BSE micrograph of sample –3.15 (scale = x250); a silt-rich mudstone

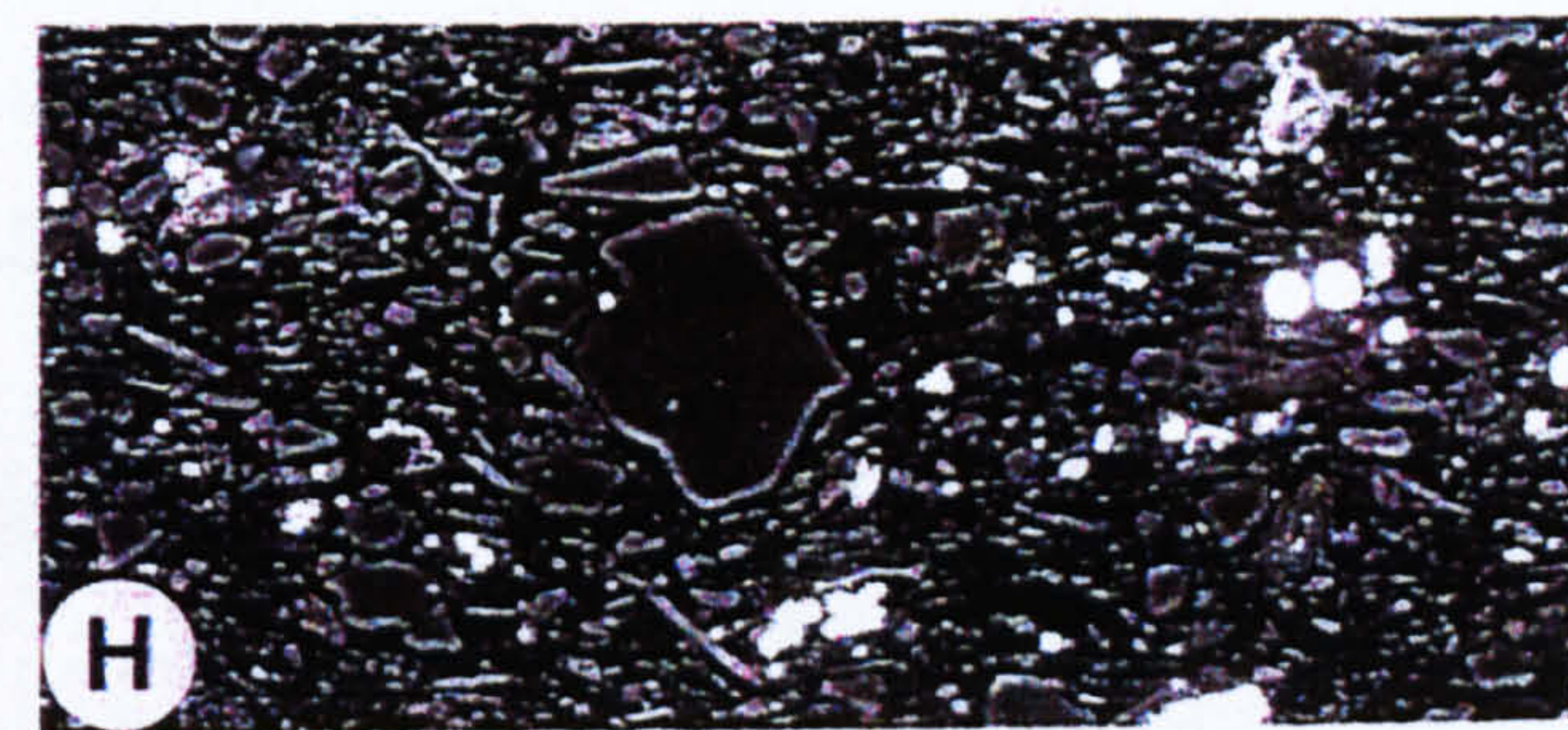
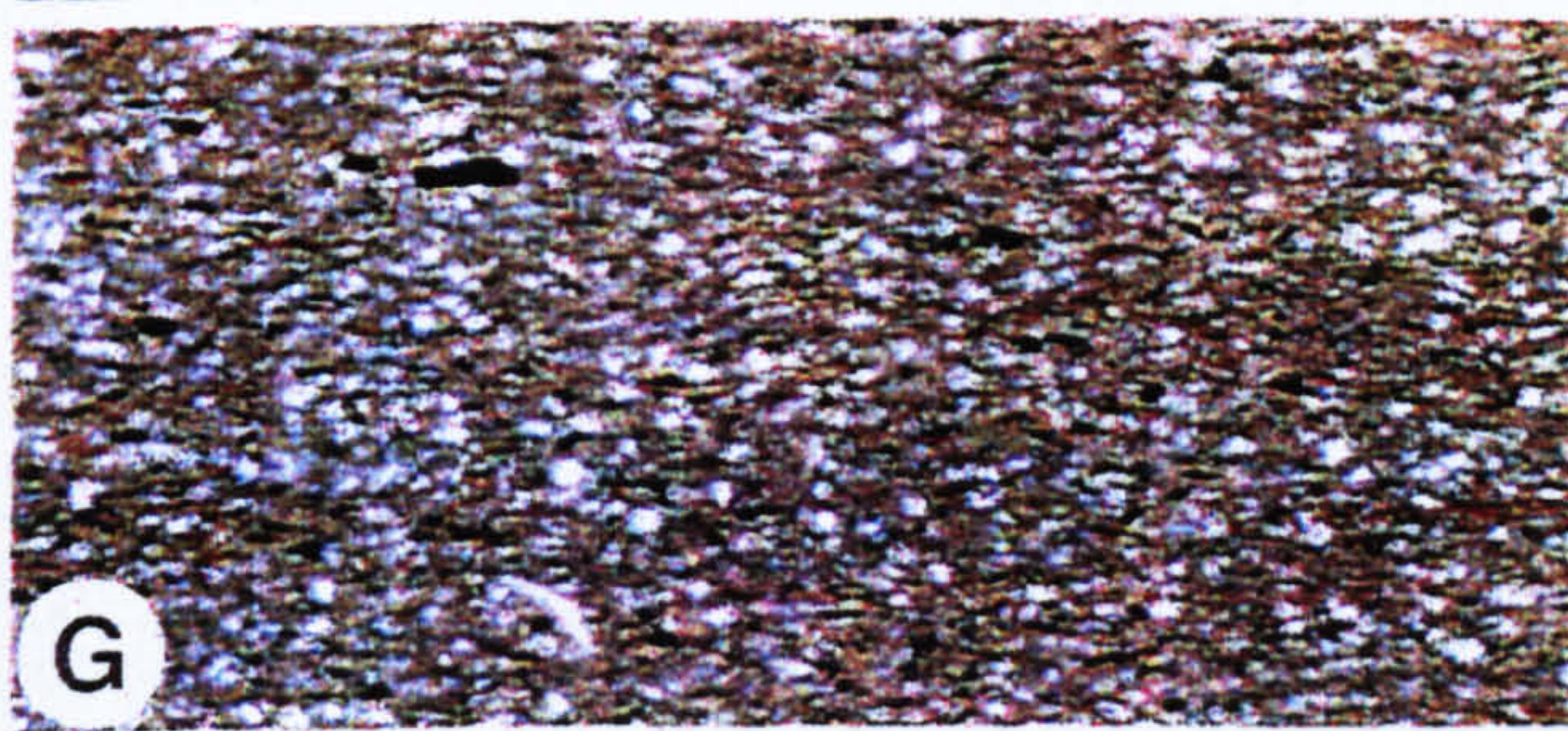
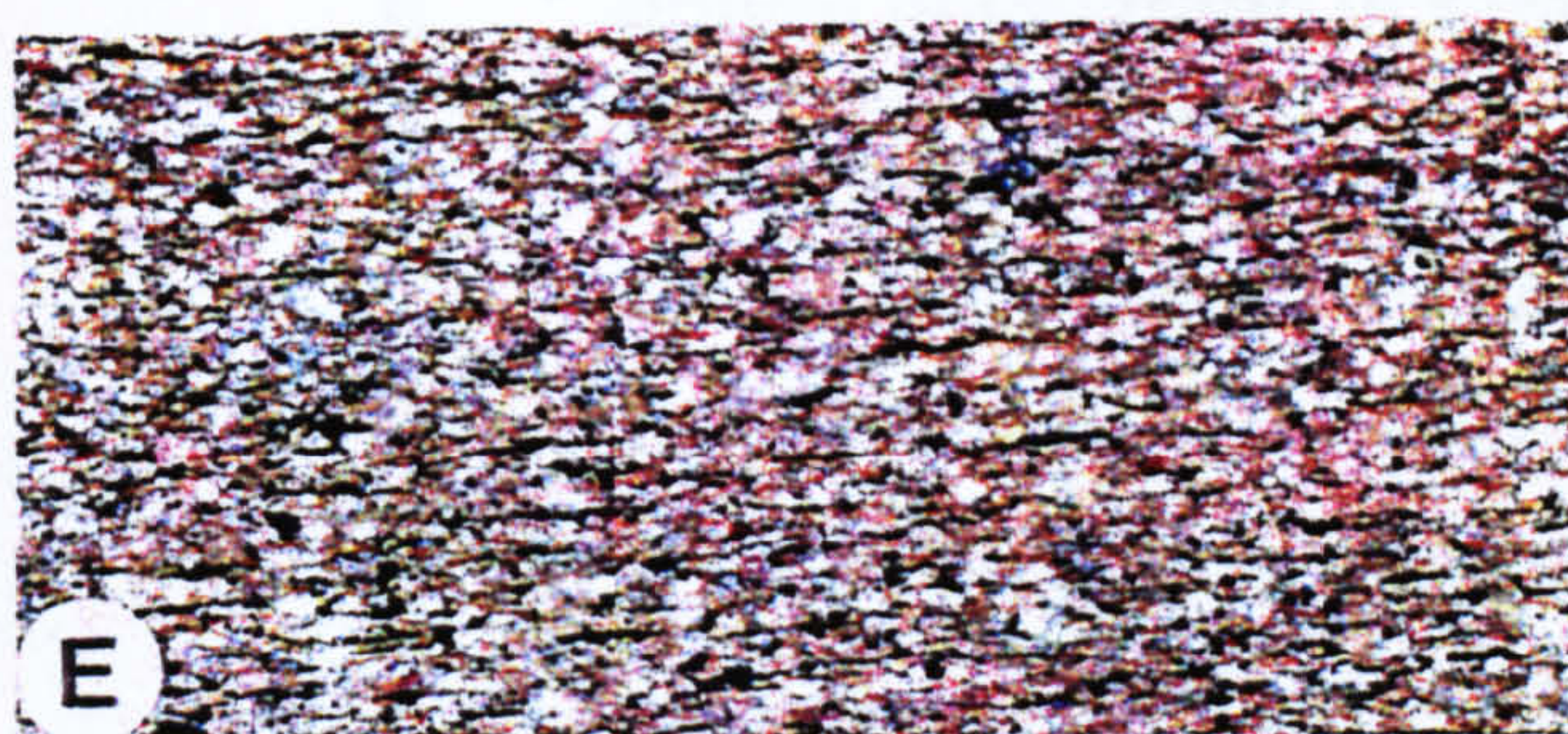
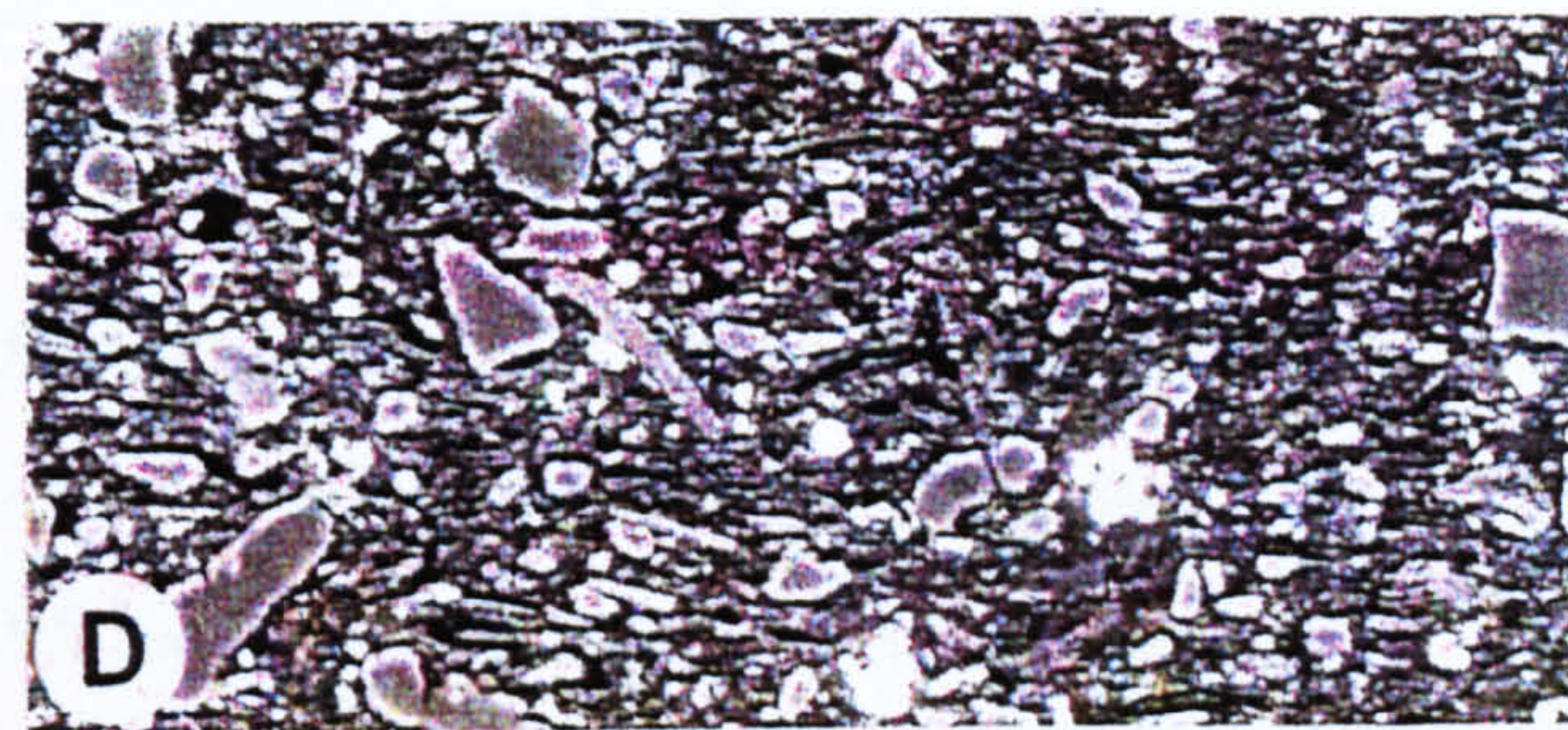
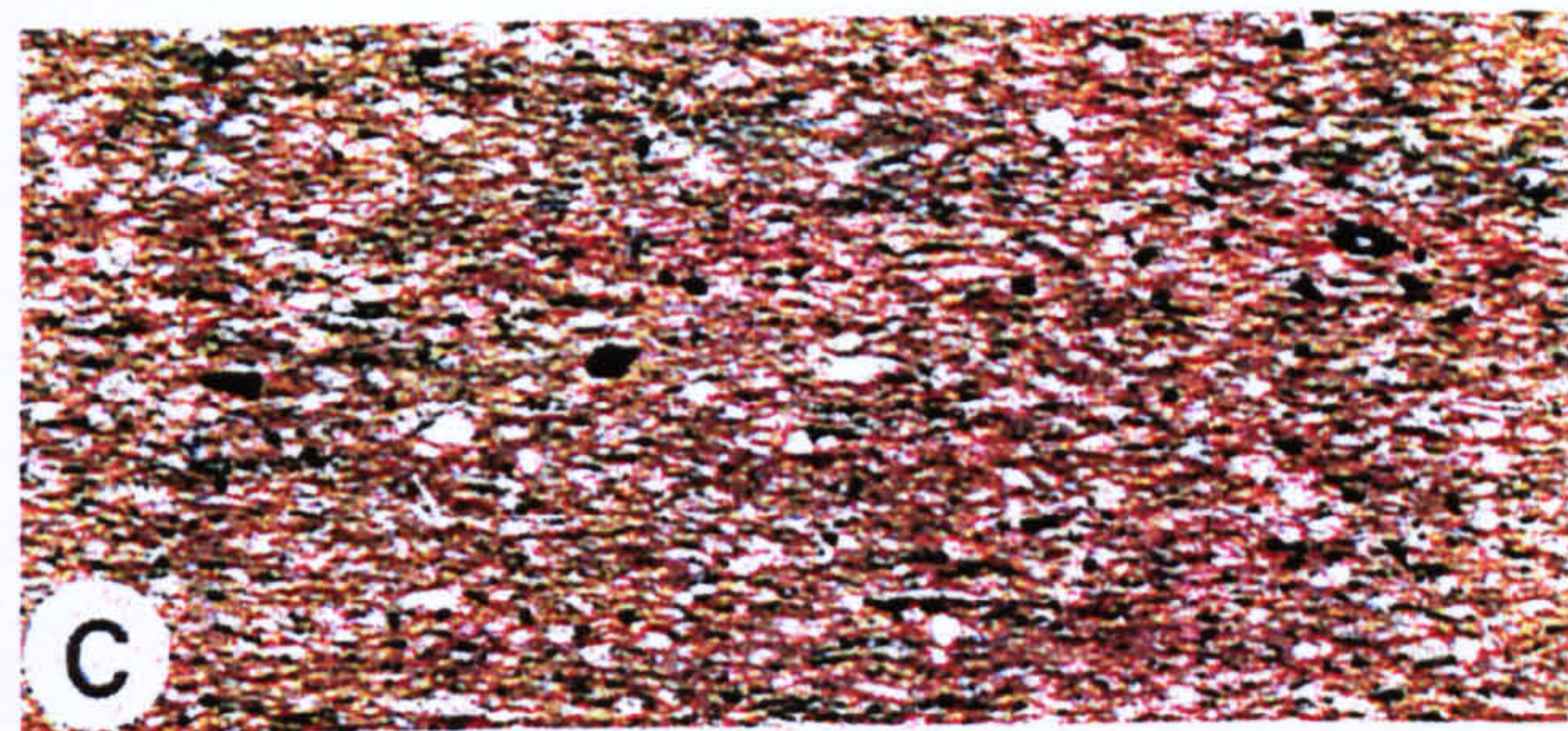
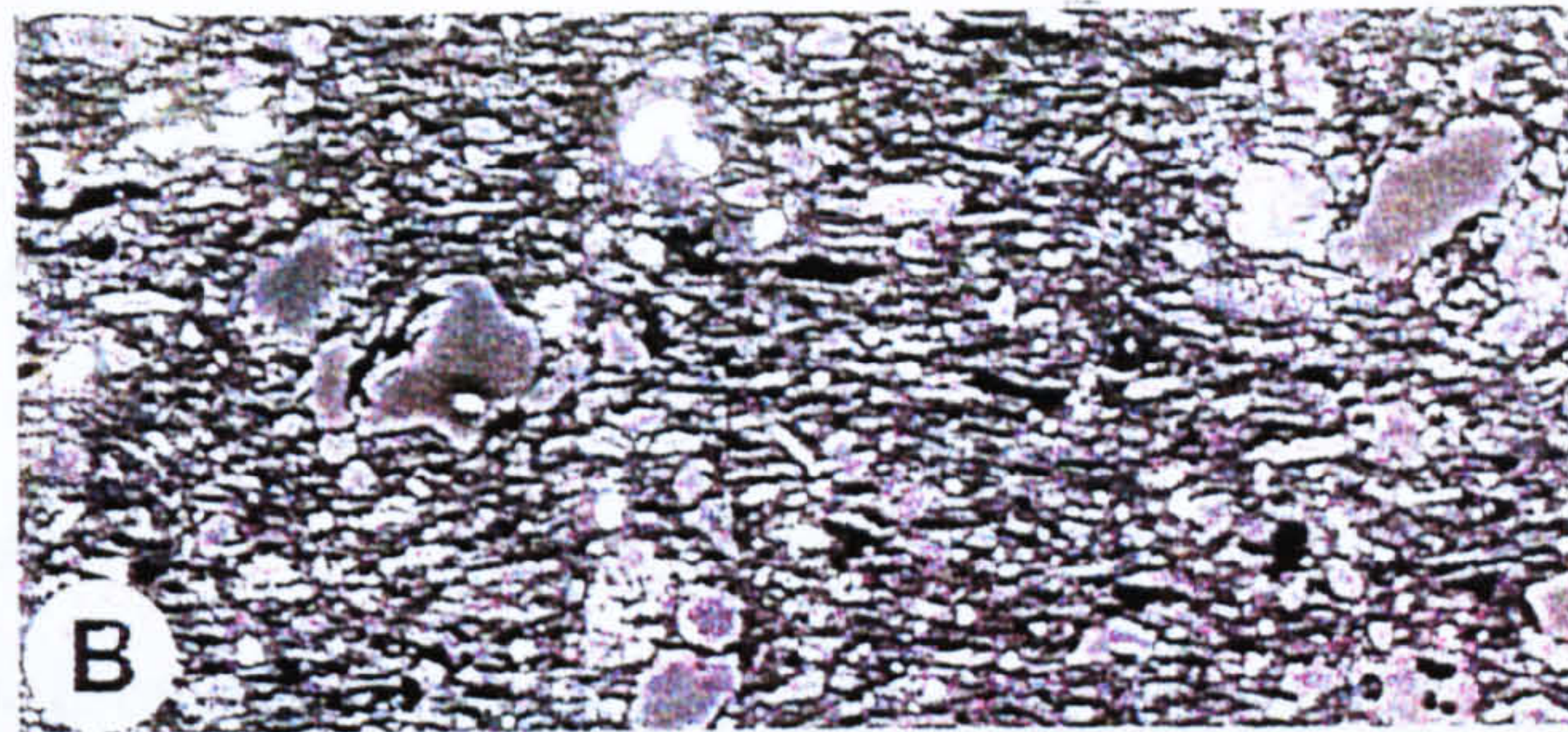


PLATE A4.4

Optical and BSE (backscattered electron) micrographs of vertical samples –1.80 to –2.55, Saxon pit (see Figure A4.1). Descriptions of the samples are given in Table A4.1.

A	optical micrograph of sample –1.80 (scale = x4); a clay-rich mudstone
B	BSE micrograph of sample –1.80 (scale = x250); a clay-rich mudstone
C	optical micrograph of sample –1.95 (scale = x4); a silt-rich mudstone
D	BSE micrograph of sample –1.95 (scale = x250); a silt-rich mudstone
E	optical micrograph of sample –2.10 (scale = x4); a silt-rich mudstone
F	BSE micrograph of sample –2.10 (scale = x250); a silt-rich mudstone
G	optical micrograph of sample –2.25 (scale = x4); a silt-rich mudstone
H	BSE micrograph of sample –2.25 (scale = x250); a silt-rich mudstone
I	optical micrograph of sample –2.40 (scale = x4); a clay-rich mudstone
J	BSE micrograph of sample –2.40 (scale = x250); a clay-rich mudstone
K	optical micrograph of sample –2.55 (scale = x4); a clay-rich mudstone
L	BSE micrograph of sample –2.55 (scale = x250); a clay-rich mudstone

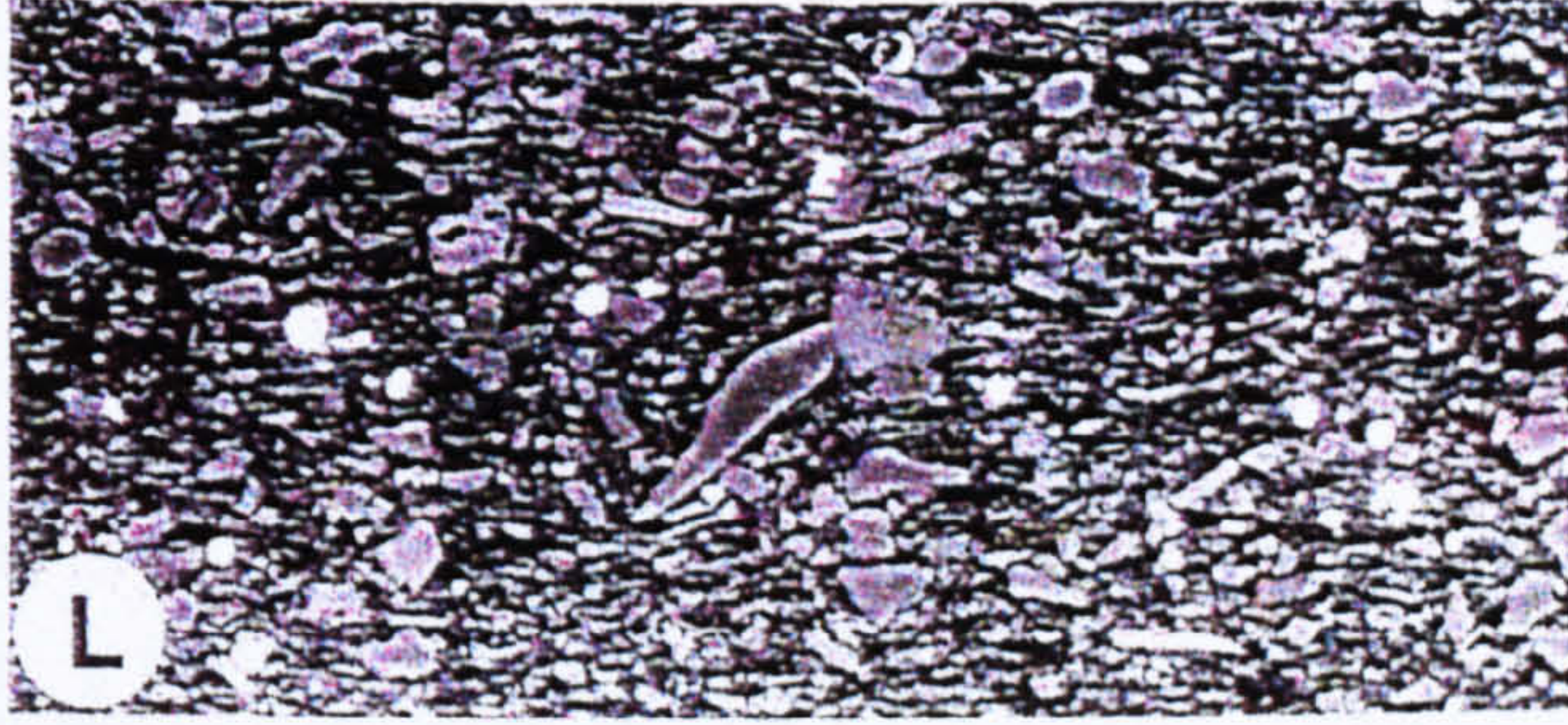
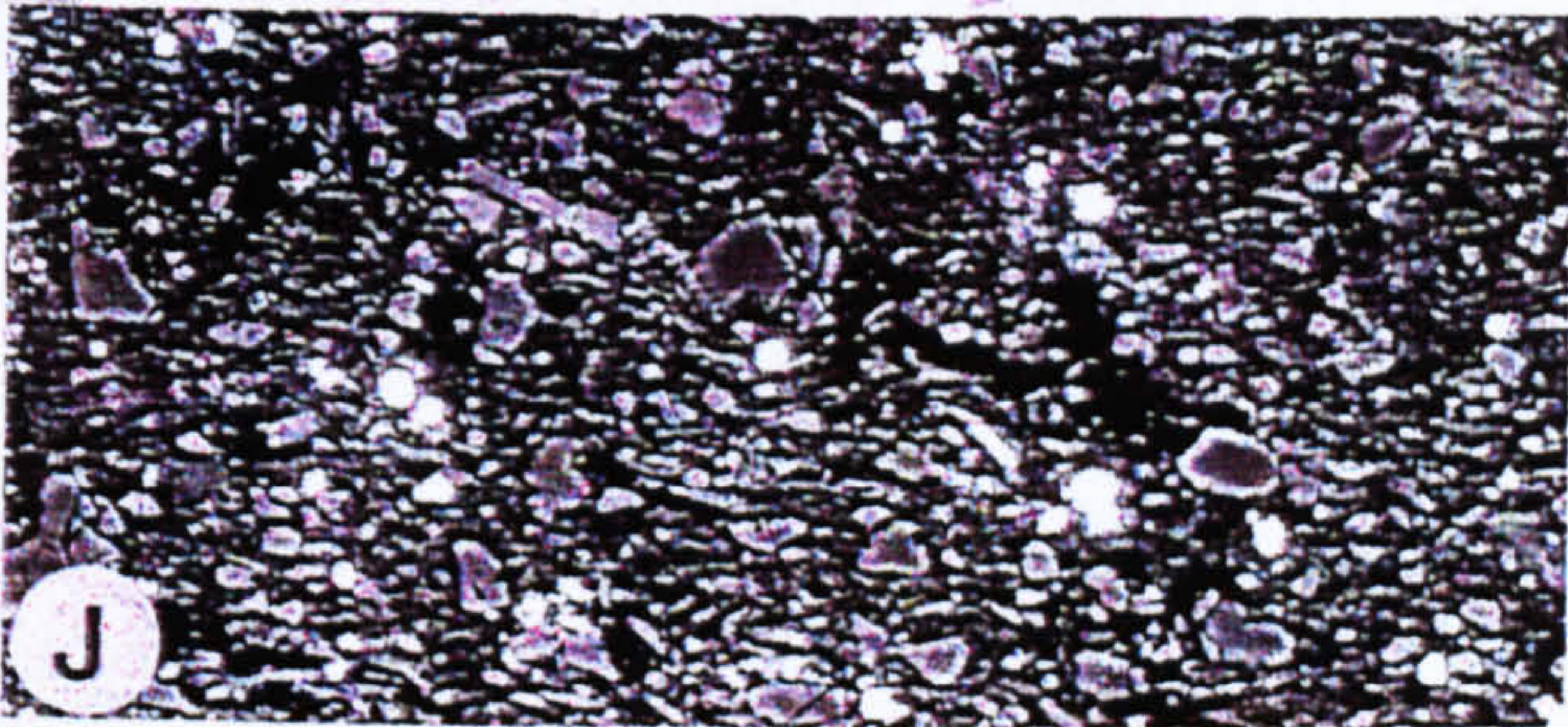
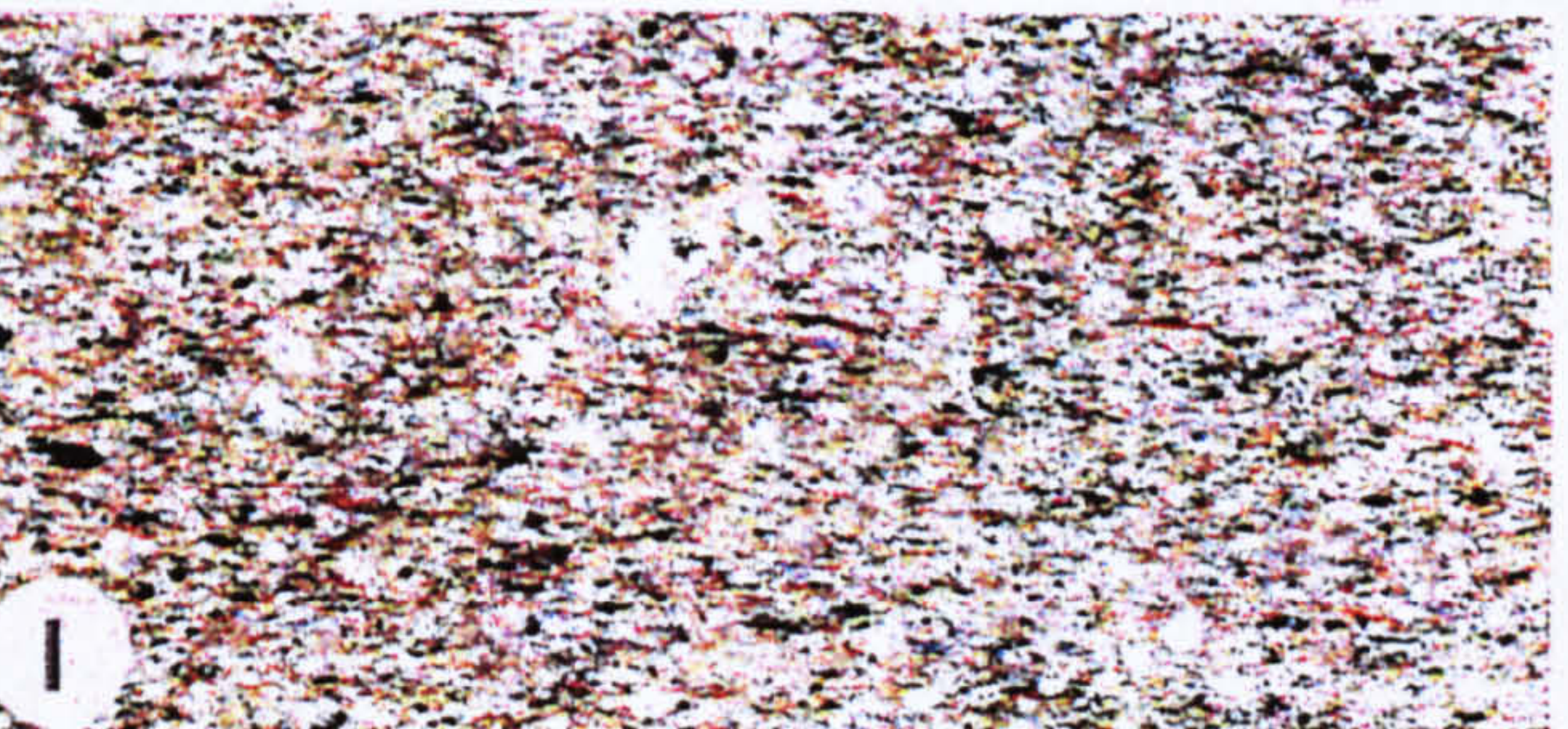
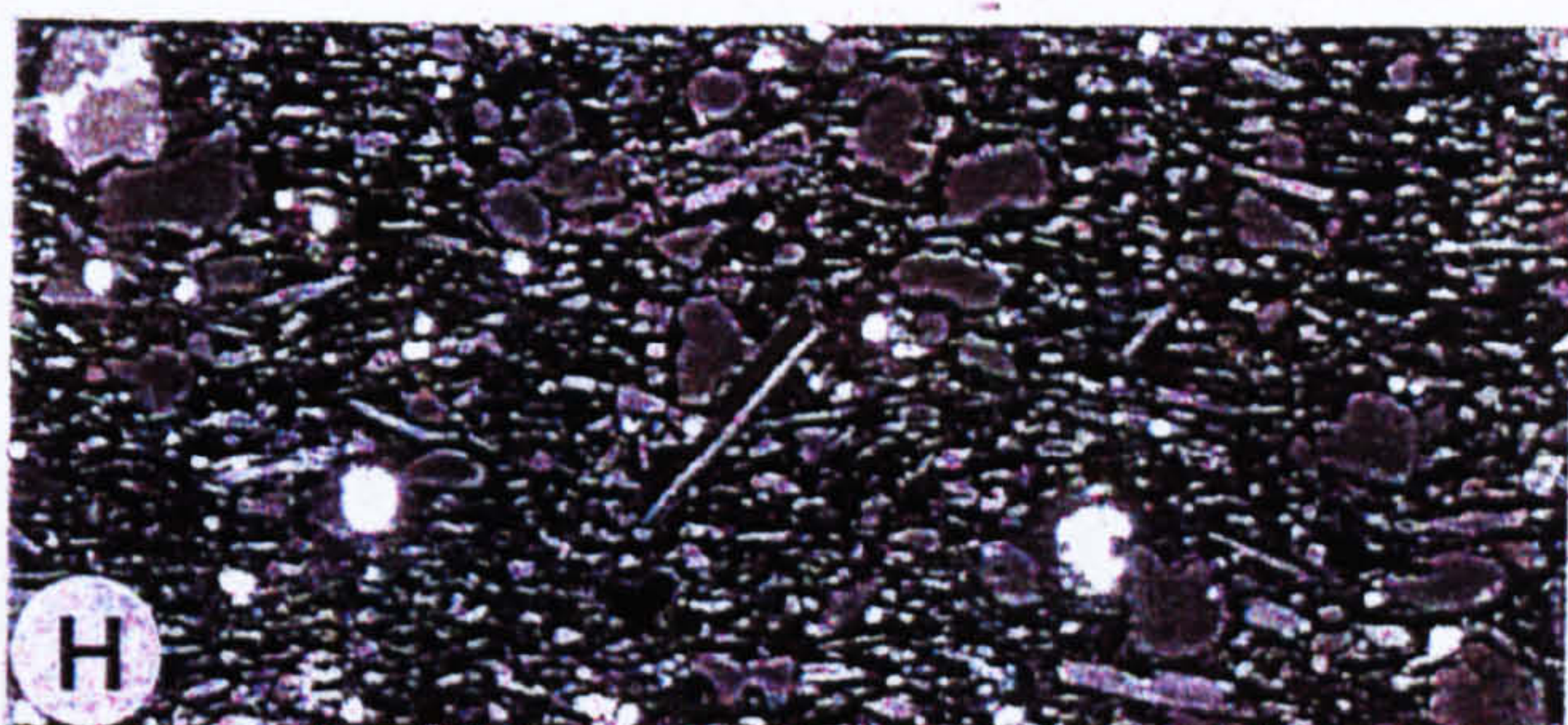
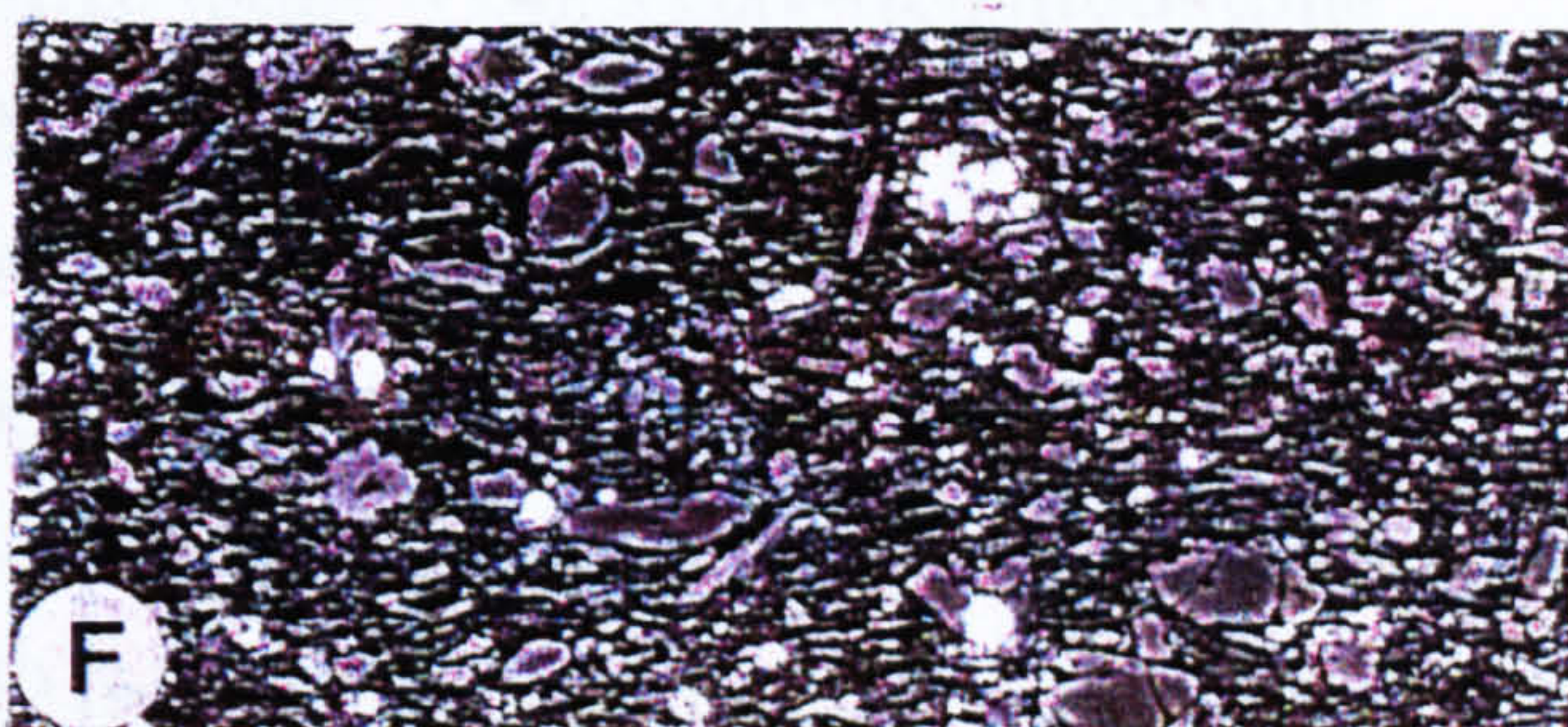
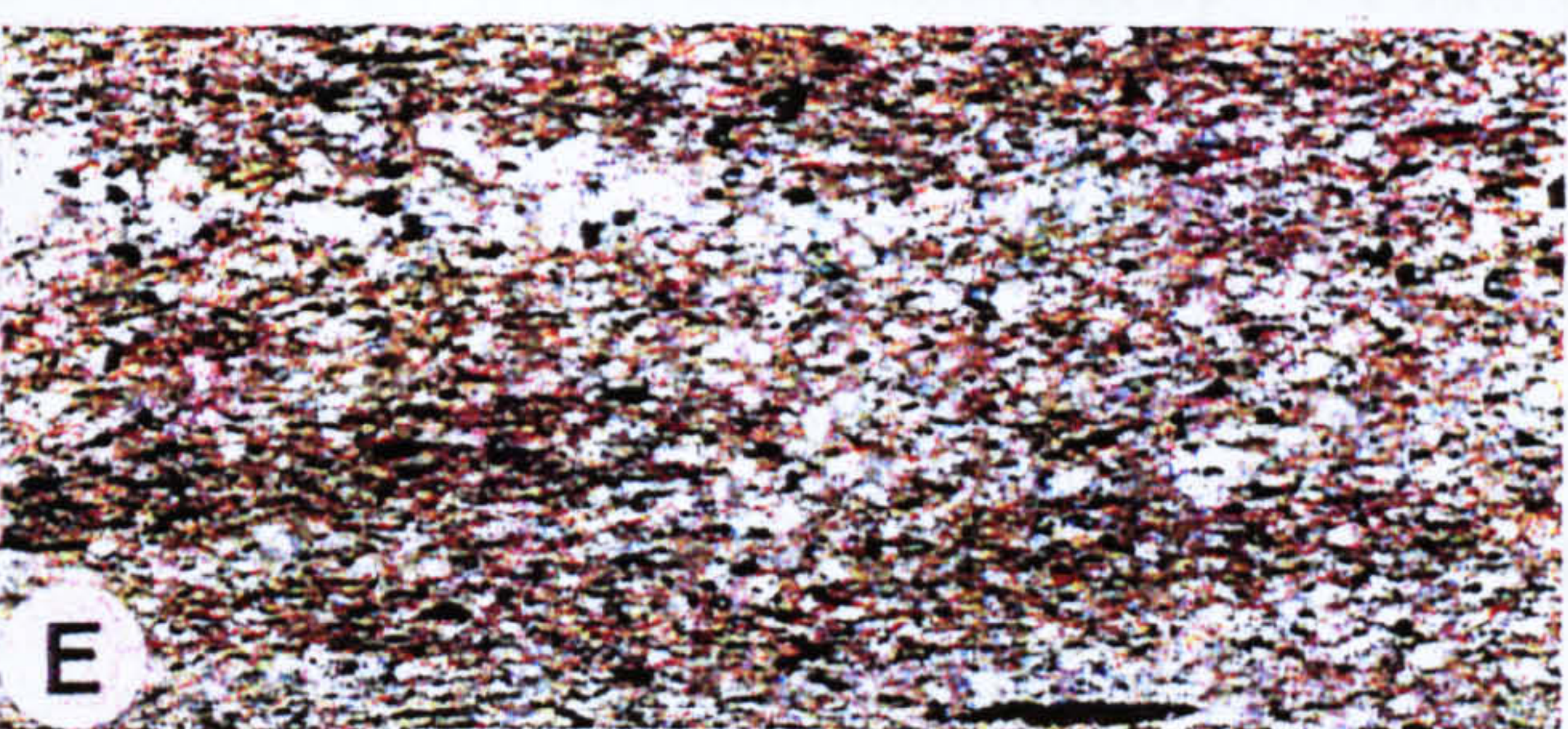
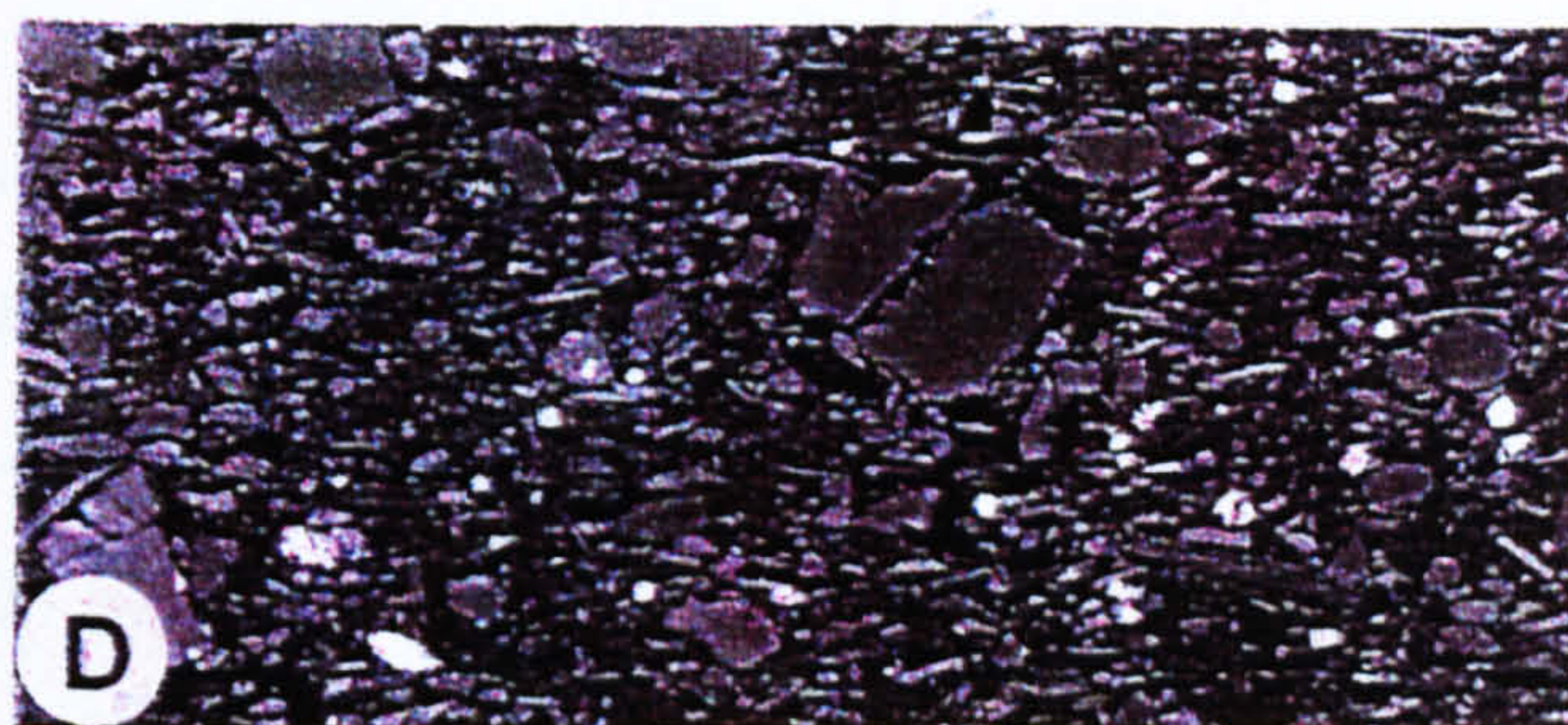
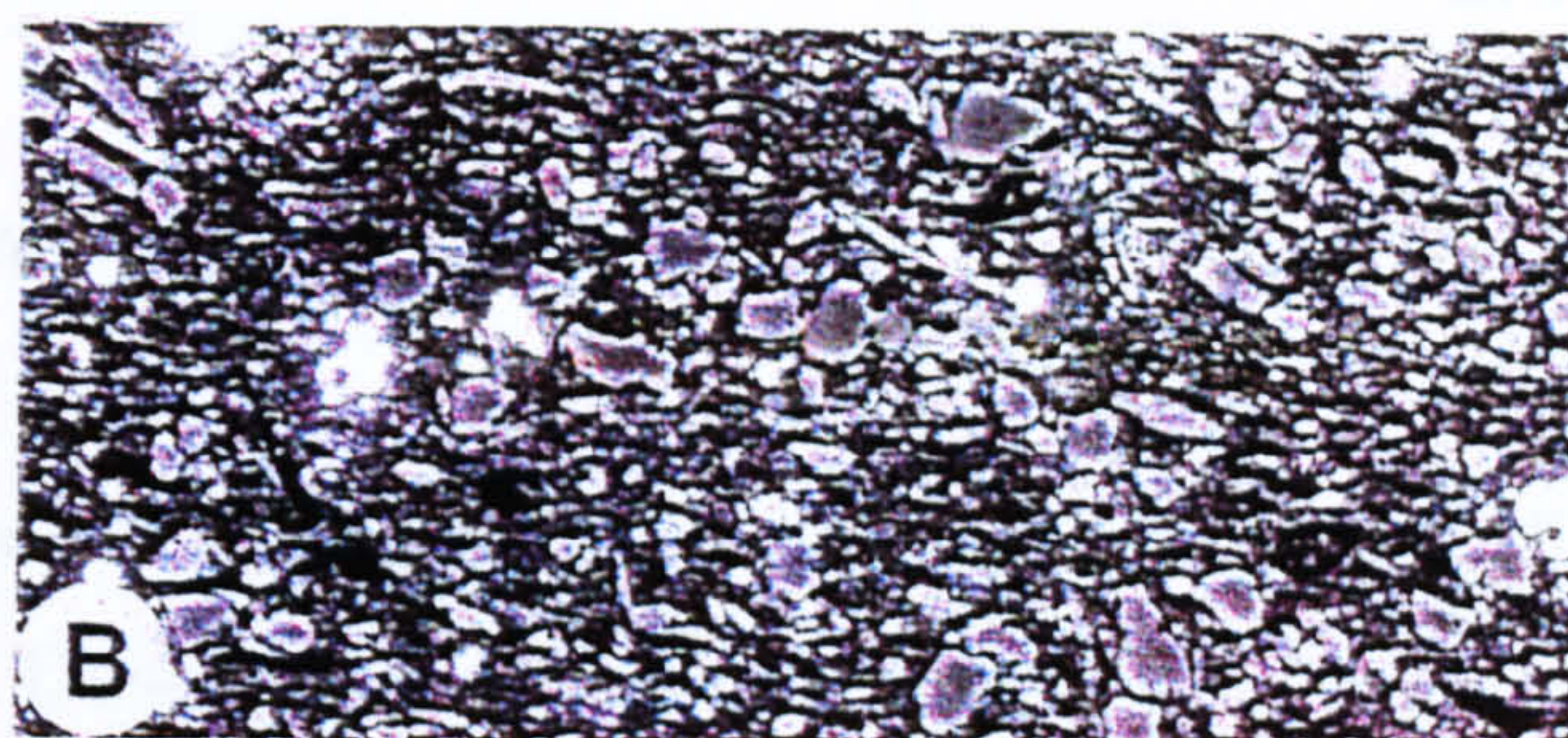


PLATE A4.5

Optical and BSE (backscattered electron) micrographs of vertical samples –0.90 to –1.65, Saxon pit (see Figure A4.1). Descriptions of the samples are given in Table A4.1.

- A optical micrograph of sample –0.90 (scale = x4); a silt-rich mudstone
- B BSE micrograph of sample –0.90 (scale = x250); a silt-rich mudstone
- C optical micrograph of sample –1.05 (scale = x4); a clay-rich mudstone
- D BSE micrograph of sample –1.05 (scale = x250); a clay-rich mudstone
- E optical micrograph of sample –1.20 (scale = x4); a clay-rich mudstone
- F BSE micrograph of sample –1.20 (scale = x250); a clay-rich mudstone
- G optical micrograph of sample –1.35 (scale = x4); a silt-rich mudstone
- H BSE micrograph of sample –1.35 (scale = x250); a silt-rich mudstone
- I optical micrograph of sample –1.50 (scale = x4); a silt-rich mudstone
- J BSE micrograph of sample –1.50 (scale = x250); a silt-rich mudstone
- K optical micrograph of sample –1.65 (scale = x4); a silt-rich mudstone
- L BSE micrograph of sample –1.65 (scale = x250); a silt-rich mudstone

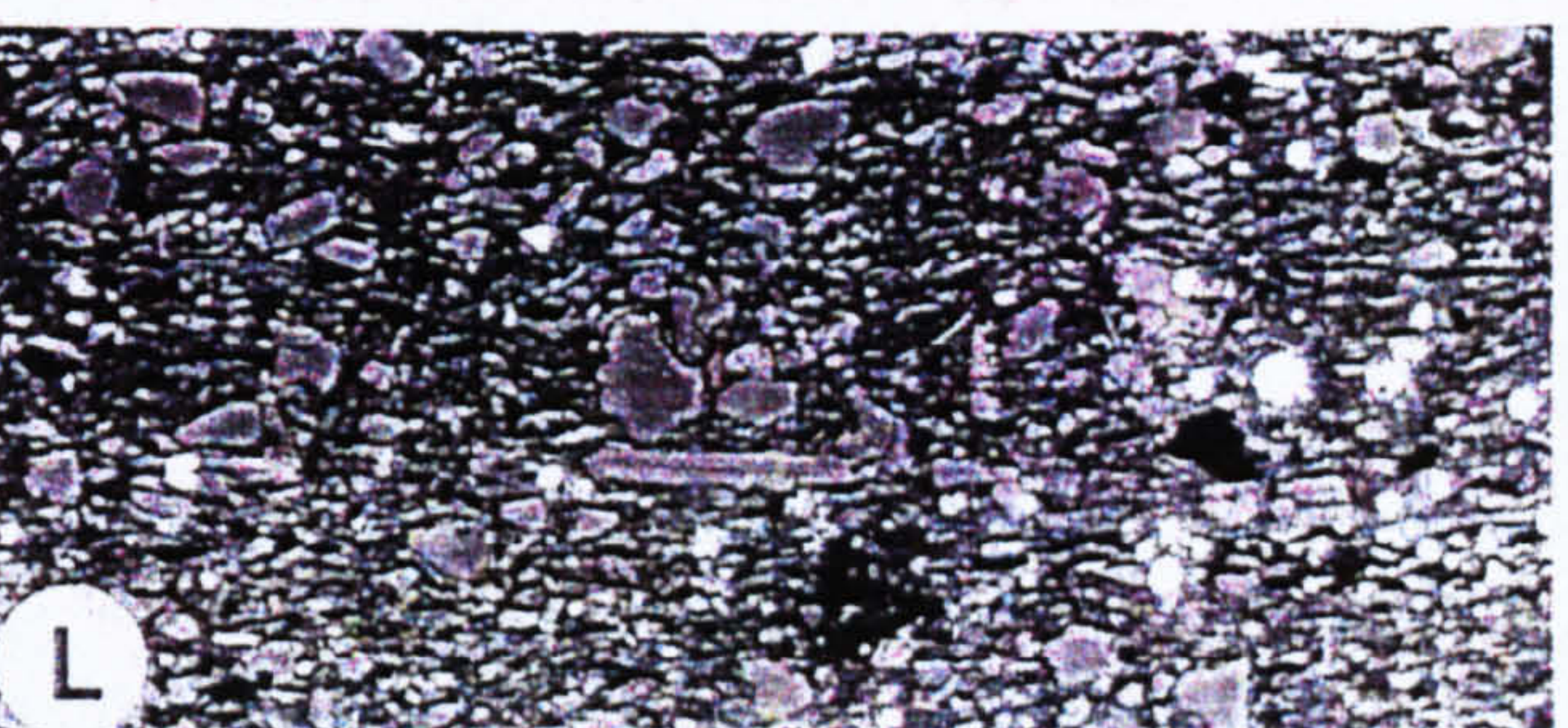
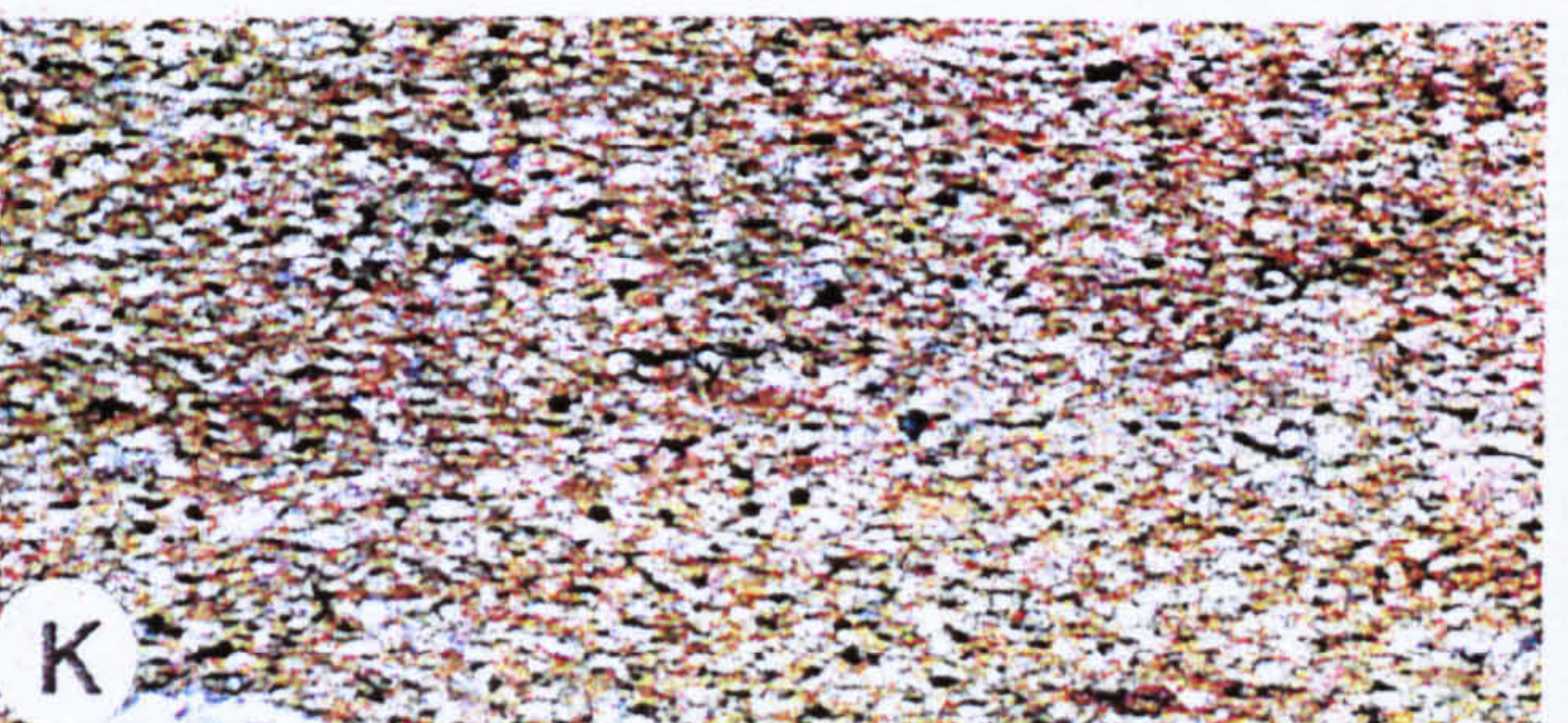
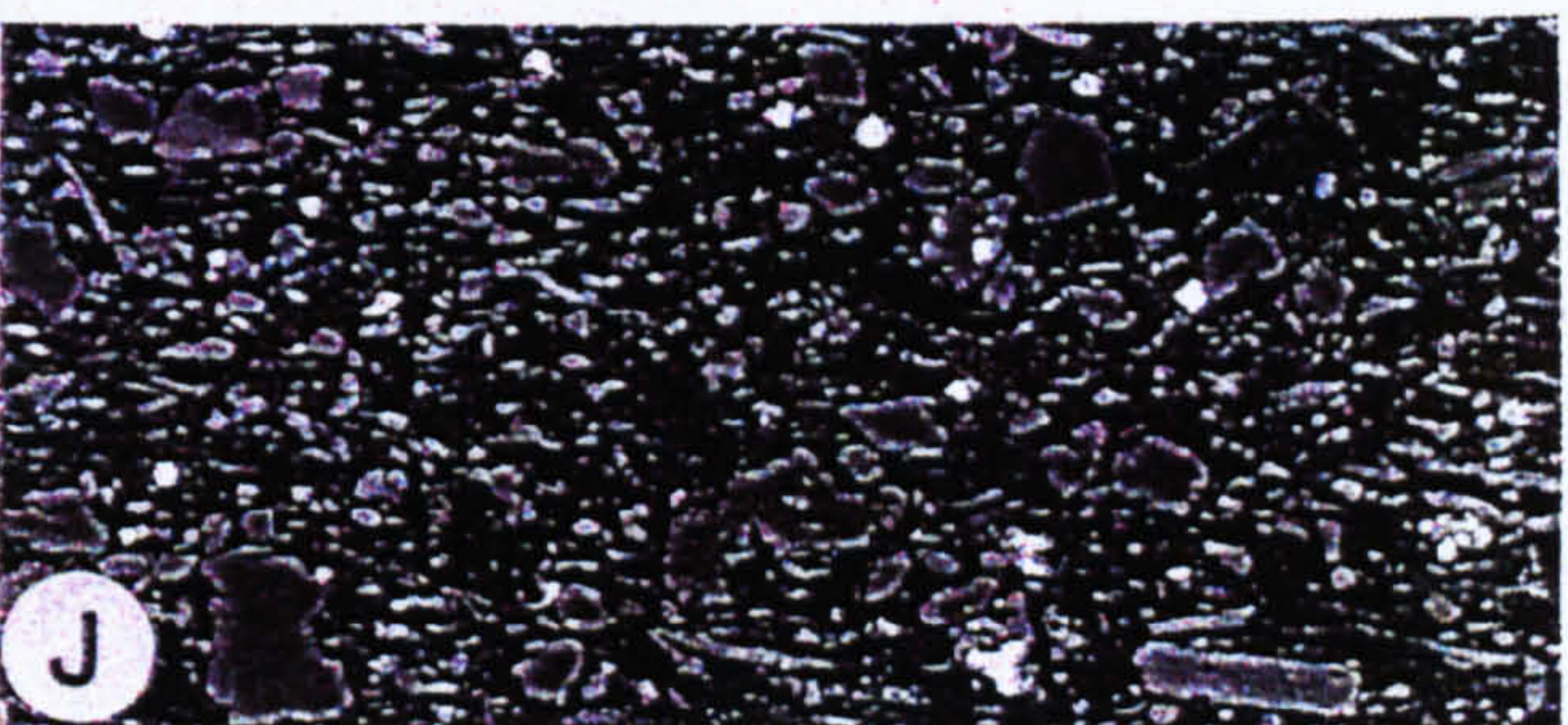
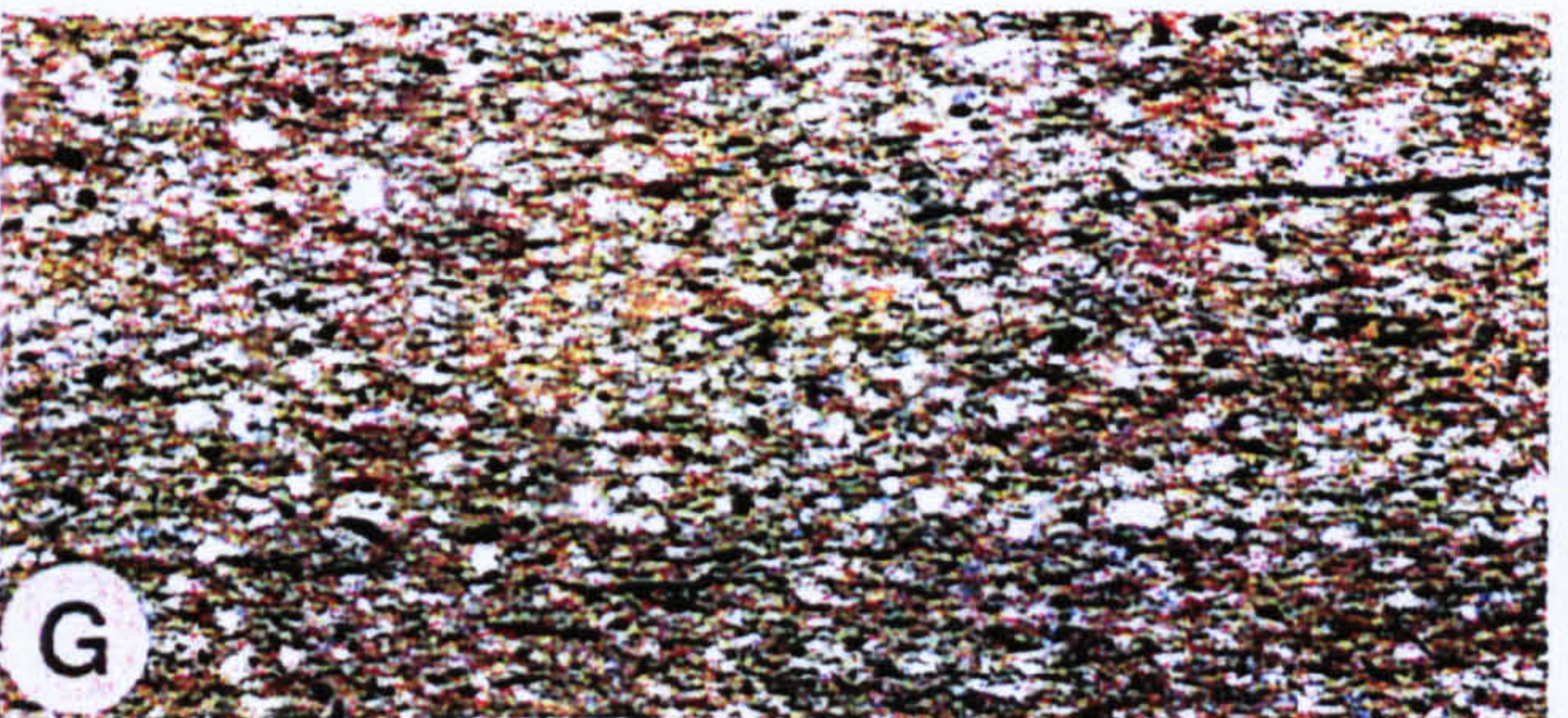
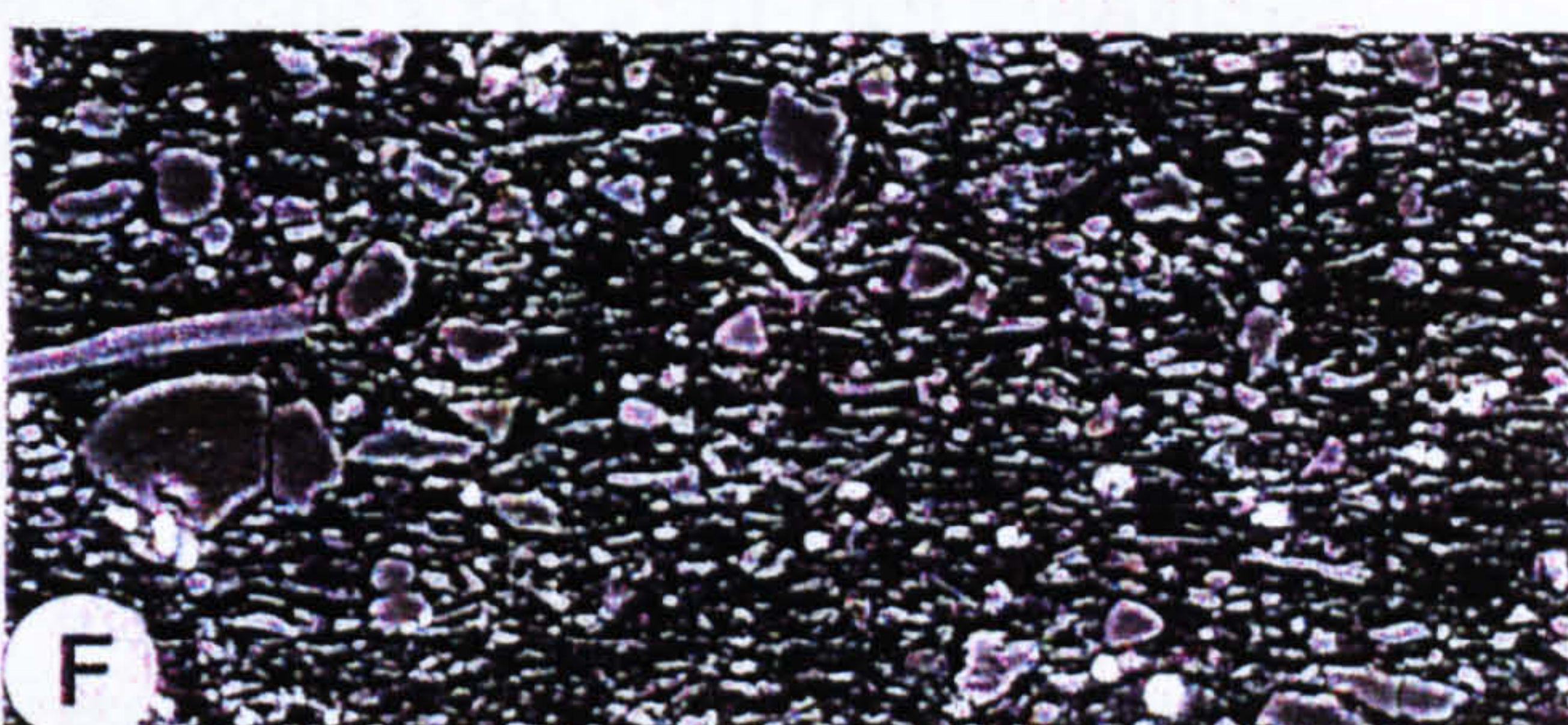
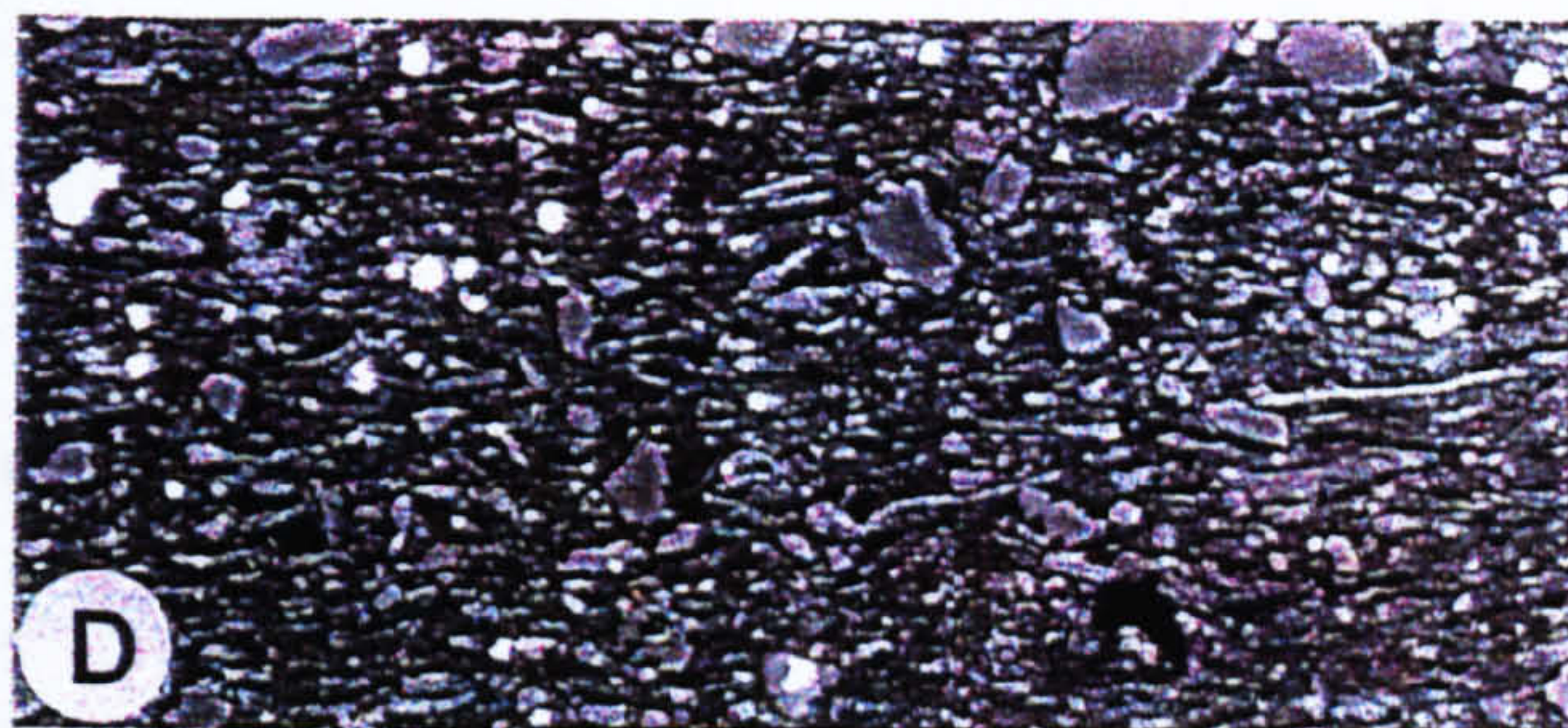
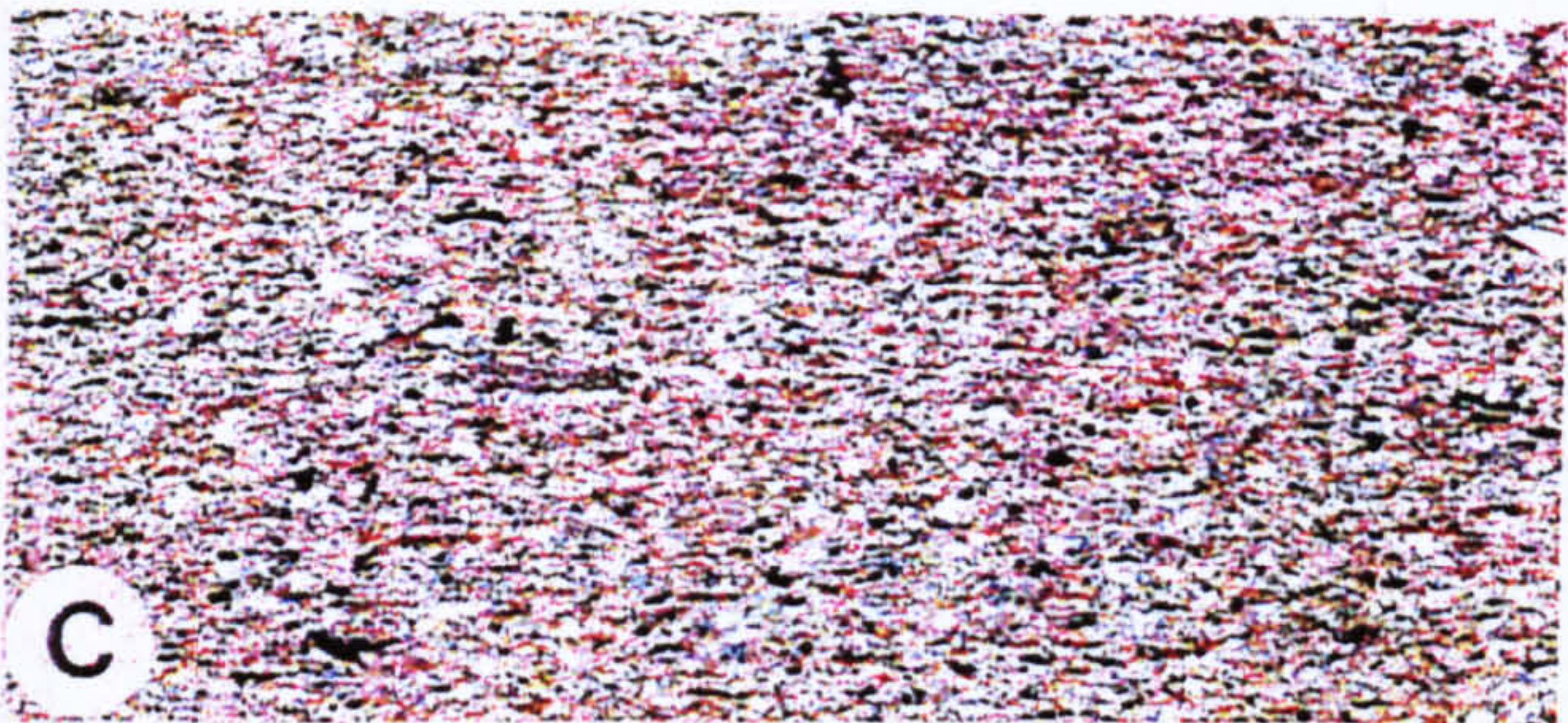


PLATE A4.6

Optical and BSE (backscattered electron) micrographs of vertical samples 0.53 to –0.75, but without samples 0.07, 0.21 and 0.33, Saxon pit (see Figure A4.1). Descriptions of the samples are given in Table A4.1.

- A optical micrograph of sample 0.53 (scale = x4); a clay-rich mudstone
- B BSE micrograph of sample 0.53 (scale = x250); a clay-rich mudstone
- C optical micrograph of sample –0.15 (scale = x4); a silt-rich mudstone
- D BSE micrograph of sample –0.15 (scale = x250); a silt-rich mudstone
- E optical micrograph of sample –0.30 (scale = x4); a silt-rich mudstone
- F BSE micrograph of sample –0.30 (scale = x250); a silt-rich mudstone
- G optical micrograph of sample –0.45 (scale = x4); a silt-rich mudstone
- H BSE micrograph of sample –0.45 (scale = x250); a silt-rich mudstone
- I optical micrograph of sample –0.60 (scale = x4); a silt-rich mudstone
- J BSE micrograph of sample –0.60 (scale = x250); a silt-rich mudstone
- K optical micrograph of sample –0.75 (scale = x4); a silt-rich mudstone
- L BSE micrograph of sample –0.75 (scale = x250); a silt-rich mudstone

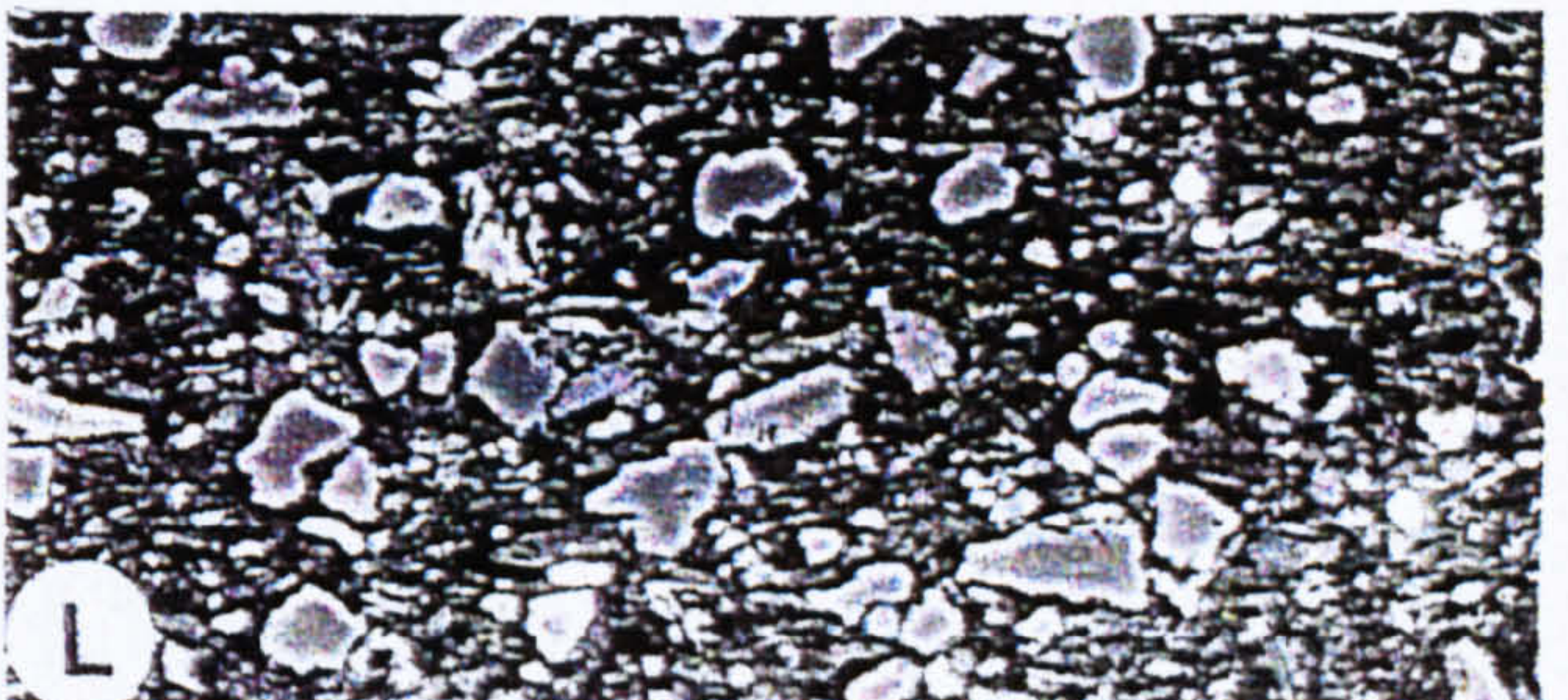
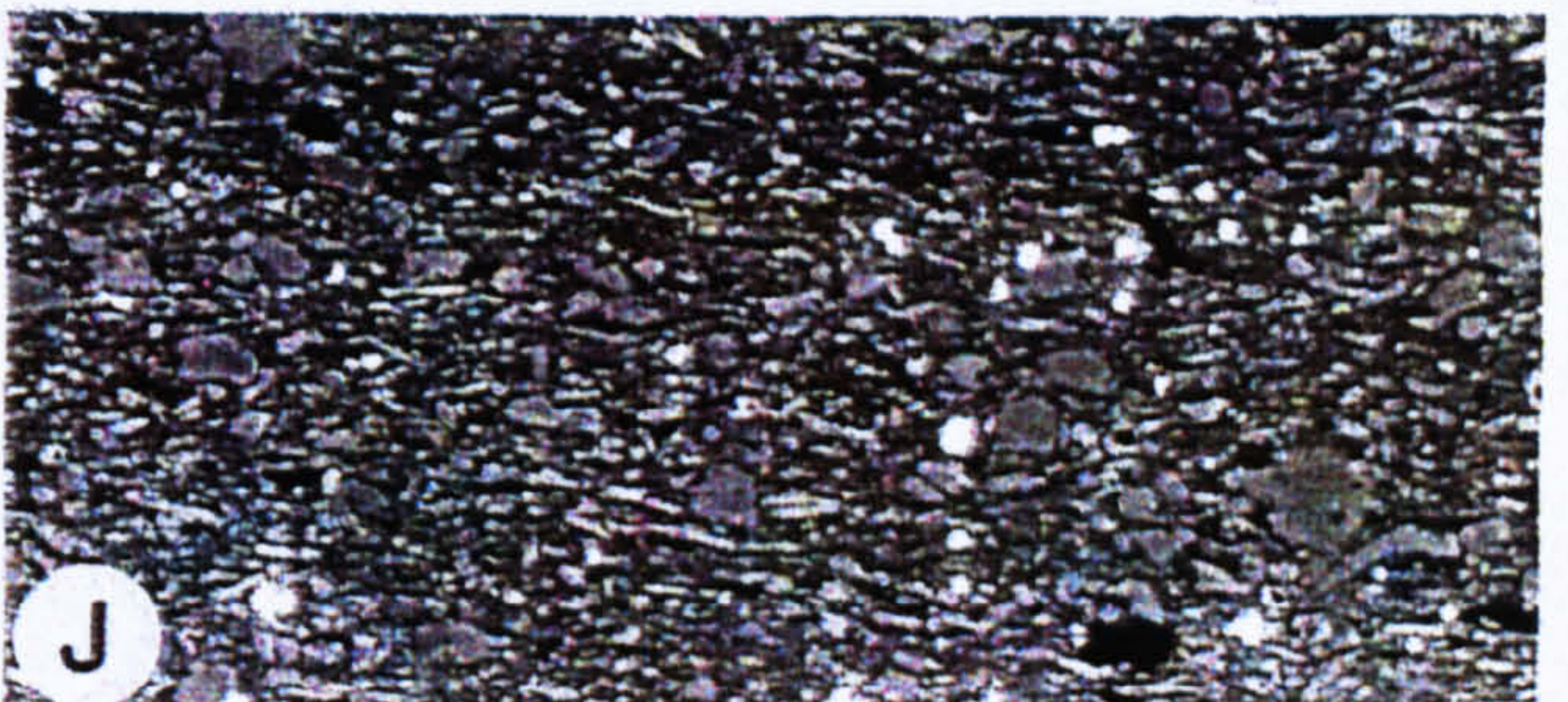
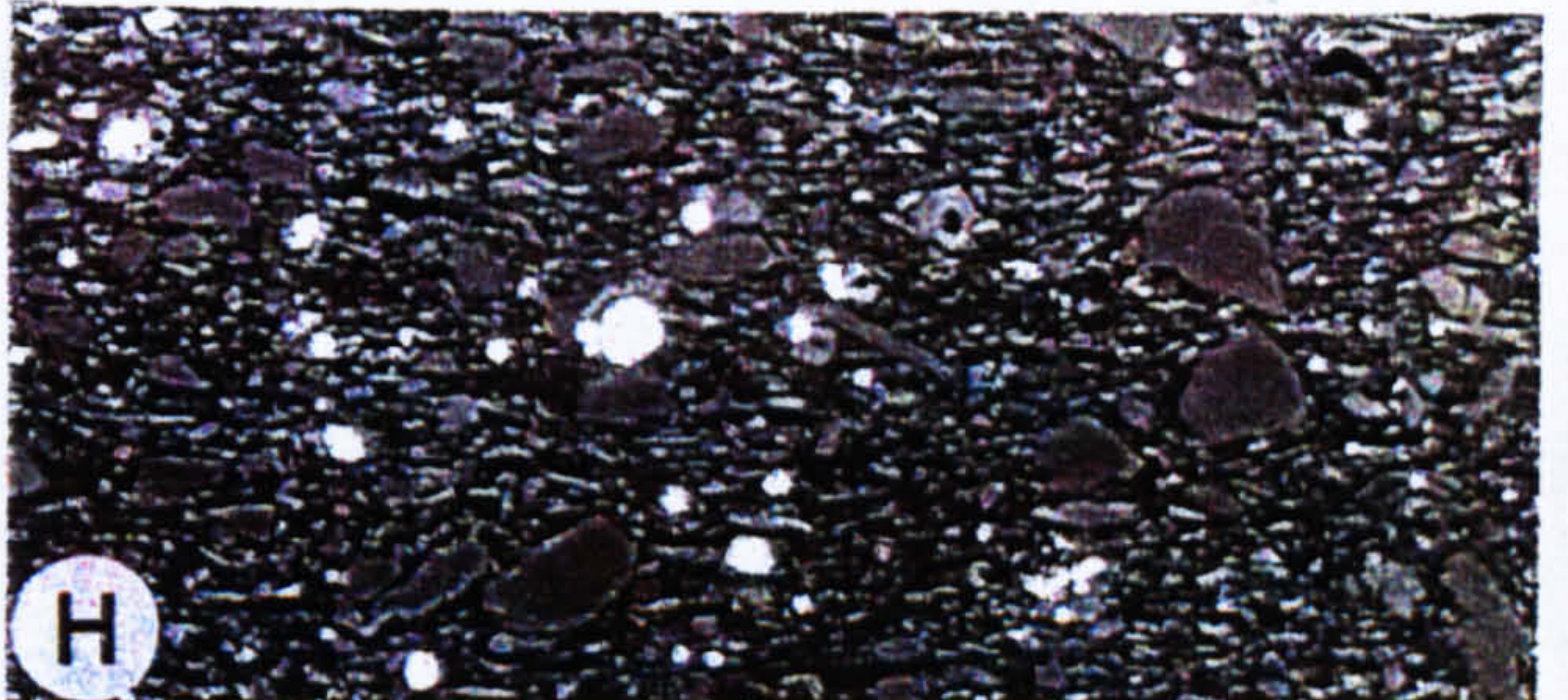
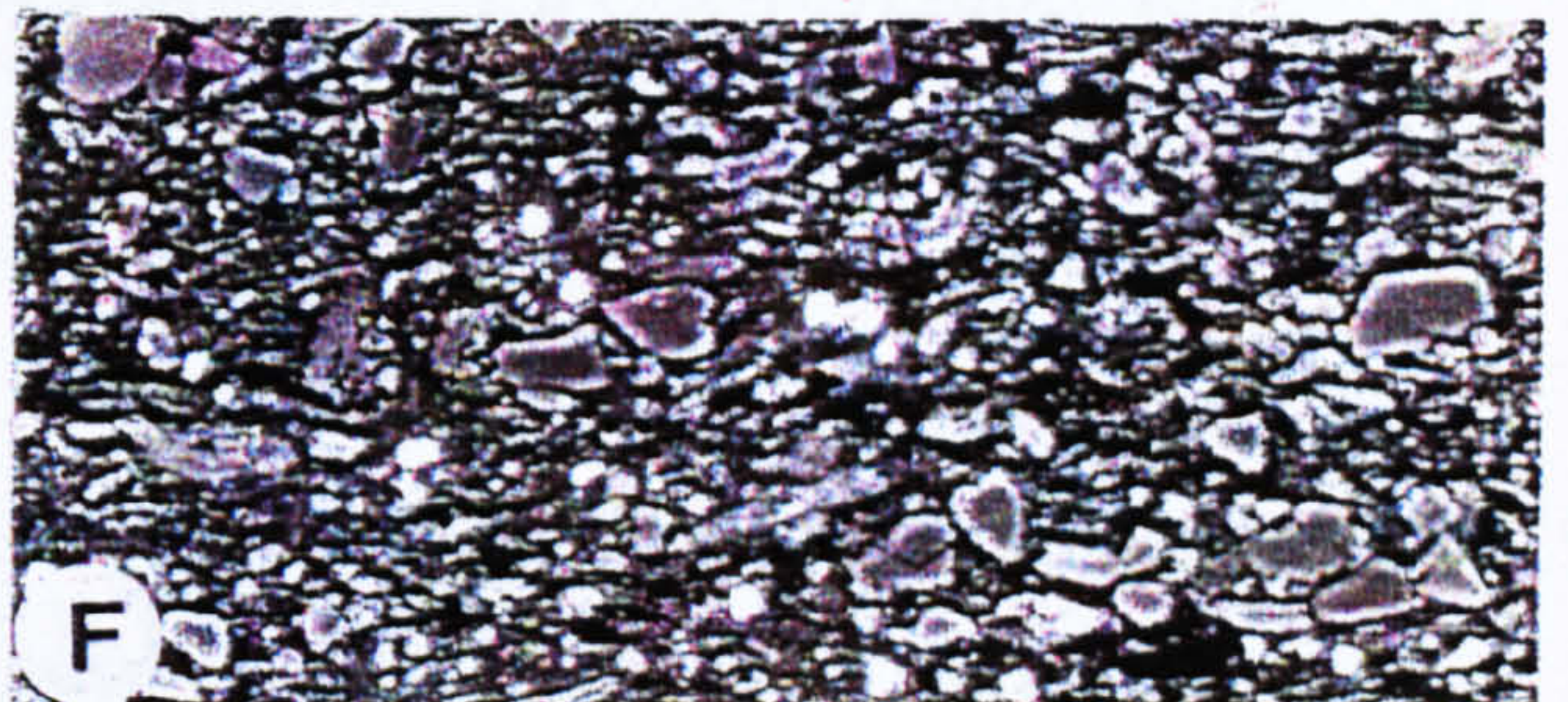
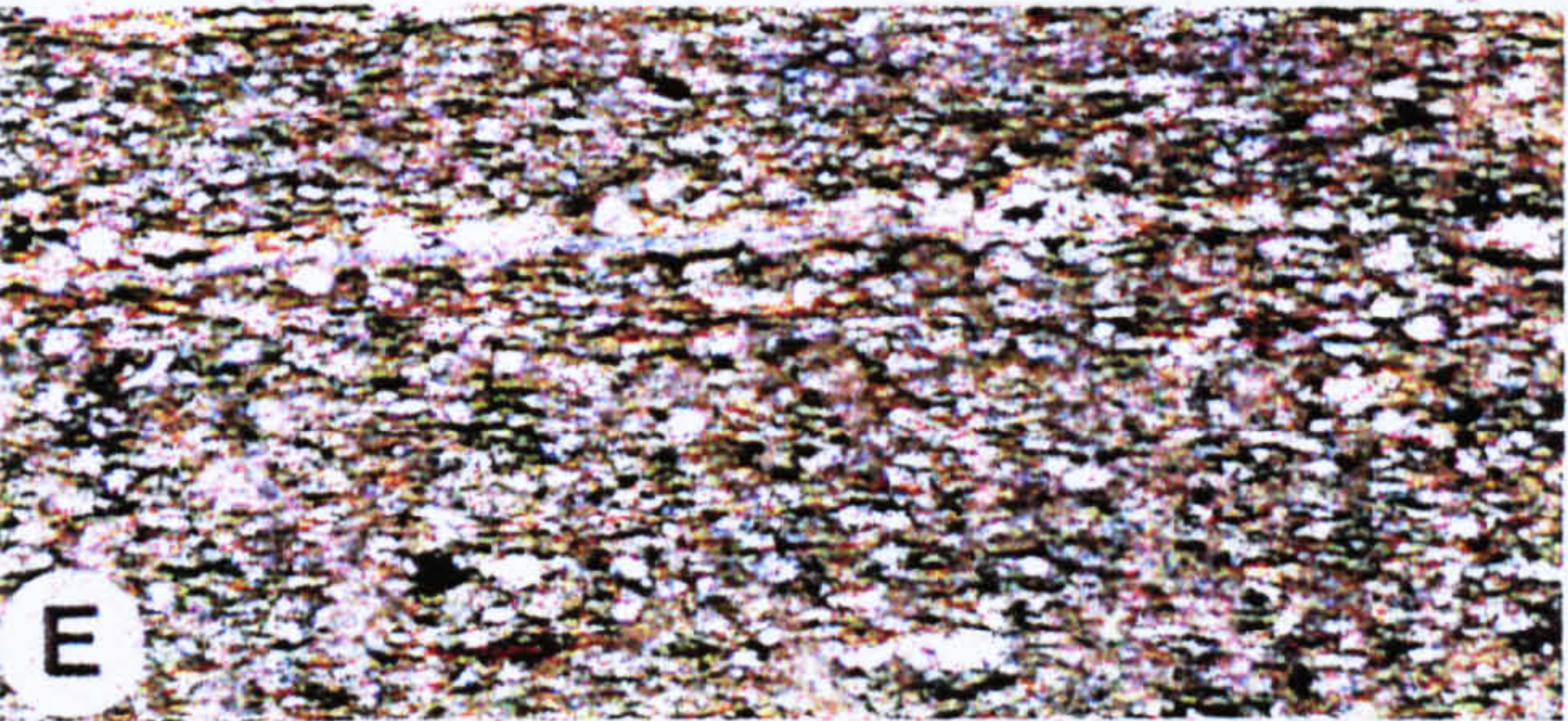
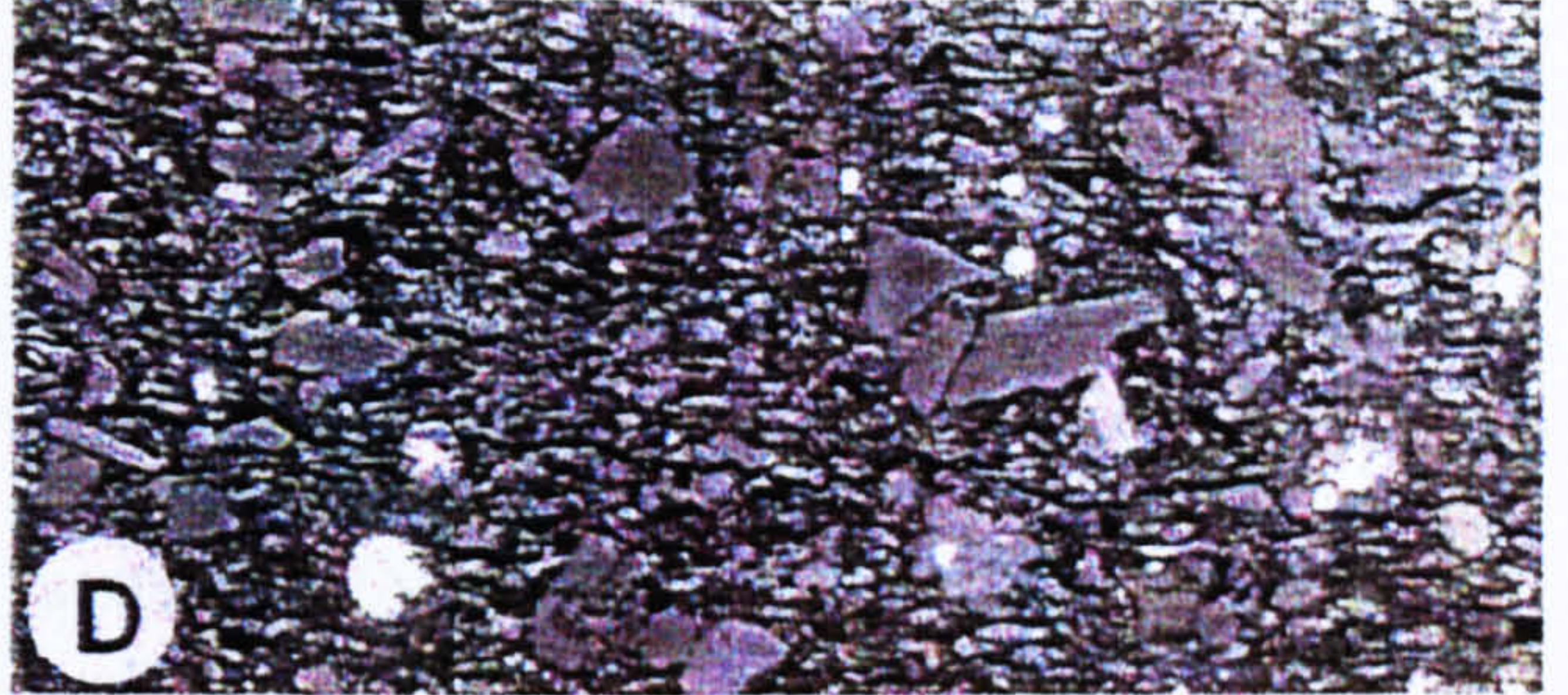
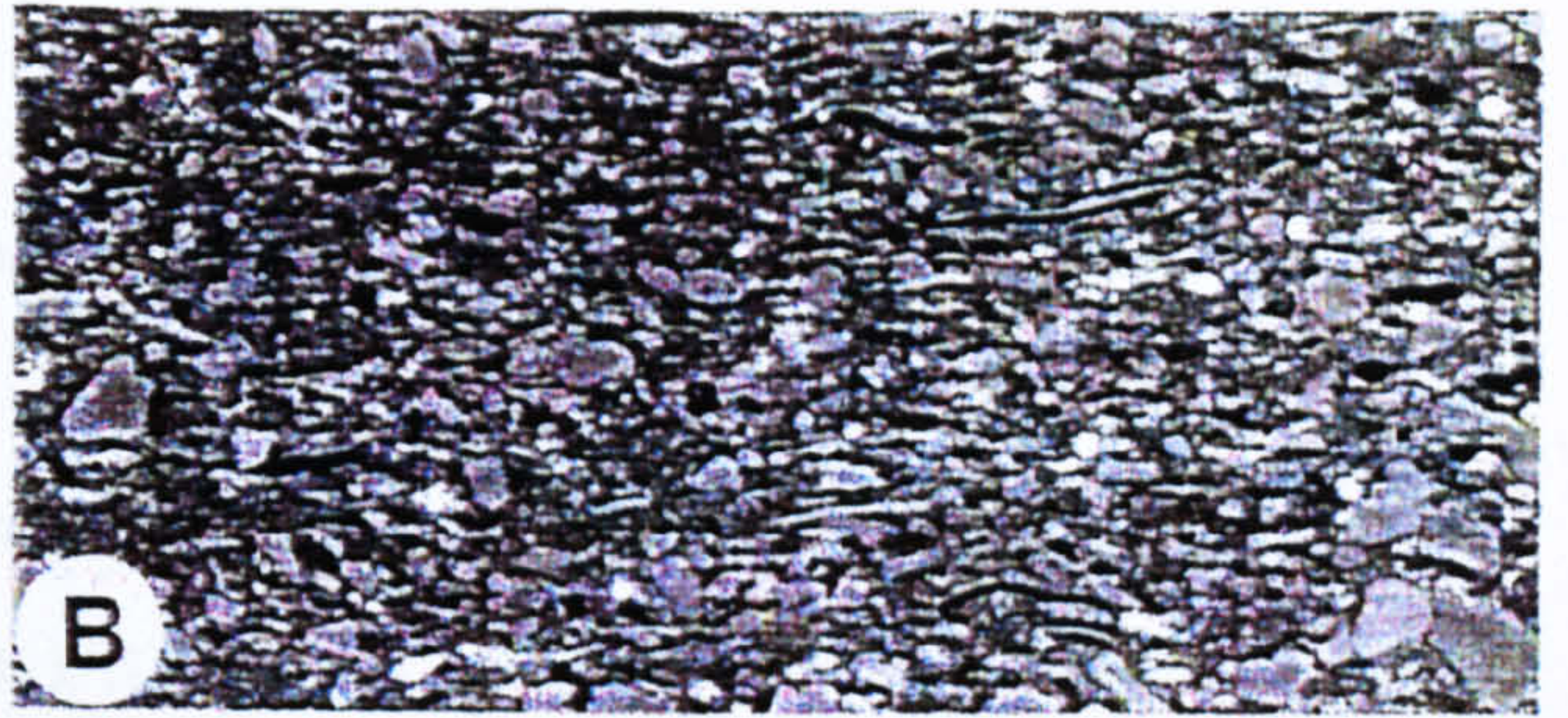
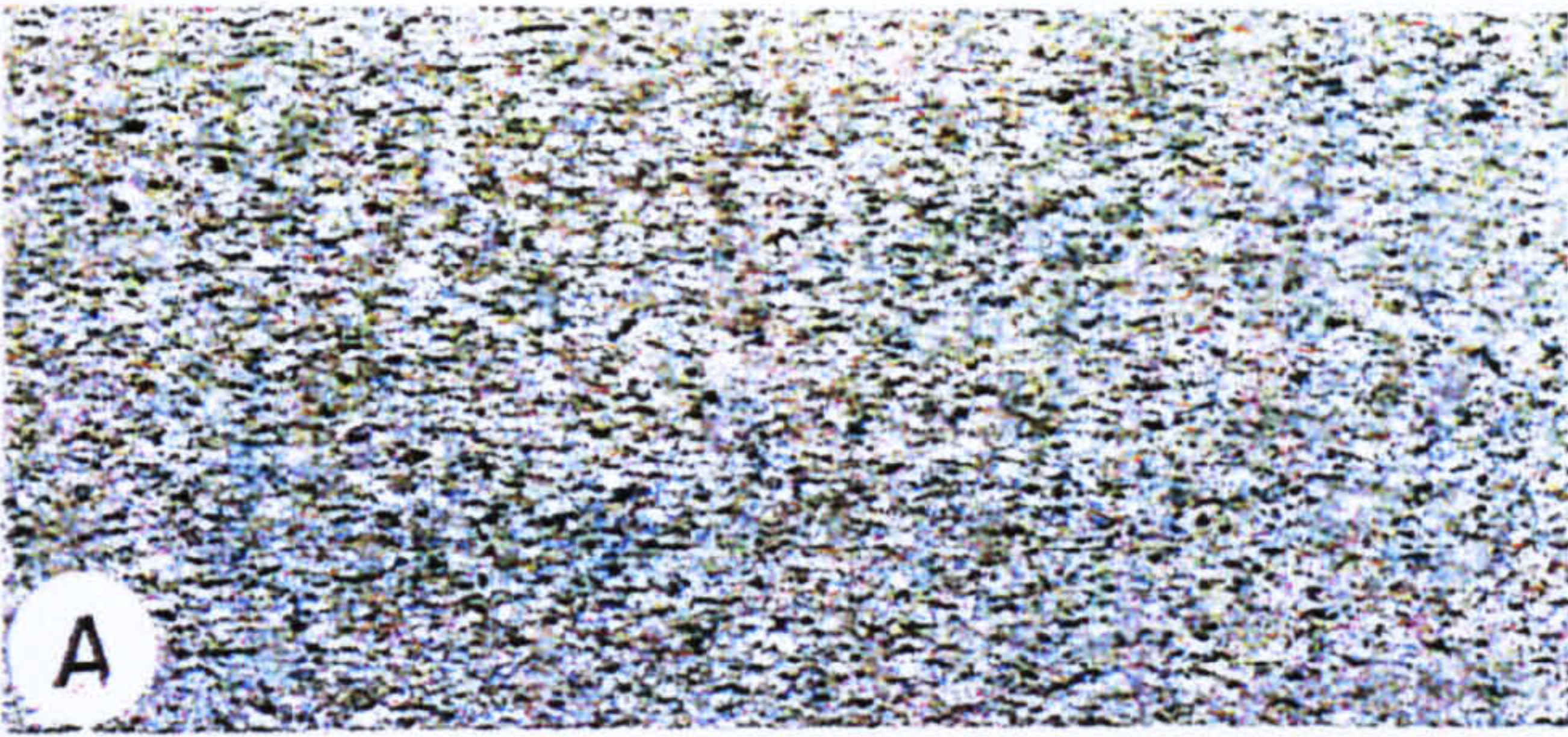


PLATE A4.7

Optical and BSE (backscattered electron) micrographs of vertical samples 1.43 to 0.68, Saxon pit (see Figure A4.1). Descriptions of the samples are given in Table A4.1.

- A optical micrograph of sample 1.43 (scale = x4); a silt-rich mudstone
- B BSE micrograph of sample 1.43 (scale = x250); a silt-rich mudstone
- C optical micrograph of sample 1.28 (scale = x4); a silt-rich mudstone
- D BSE micrograph of sample 1.28 (scale = x250); a silt-rich mudstone
- E optical micrograph of sample 1.13 (scale = x4); a clay-rich mudstone
- F BSE micrograph of sample 1.13 (scale = x250); a clay-rich mudstone
- G optical micrograph of sample 0.98 (scale = x4); a clay-rich mudstone
- H BSE micrograph of sample 0.98 (scale = x250); a clay-rich mudstone
- I optical micrograph of sample 0.83 (scale = x4); a clay-rich mudstone
- J BSE micrograph of sample 0.83 (scale = x250); a clay-rich mudstone
- K optical micrograph of sample 0.68 (scale = x4); a silt-rich mudstone
- L BSE micrograph of sample 0.68 (scale = x250); a silt-rich mudstone

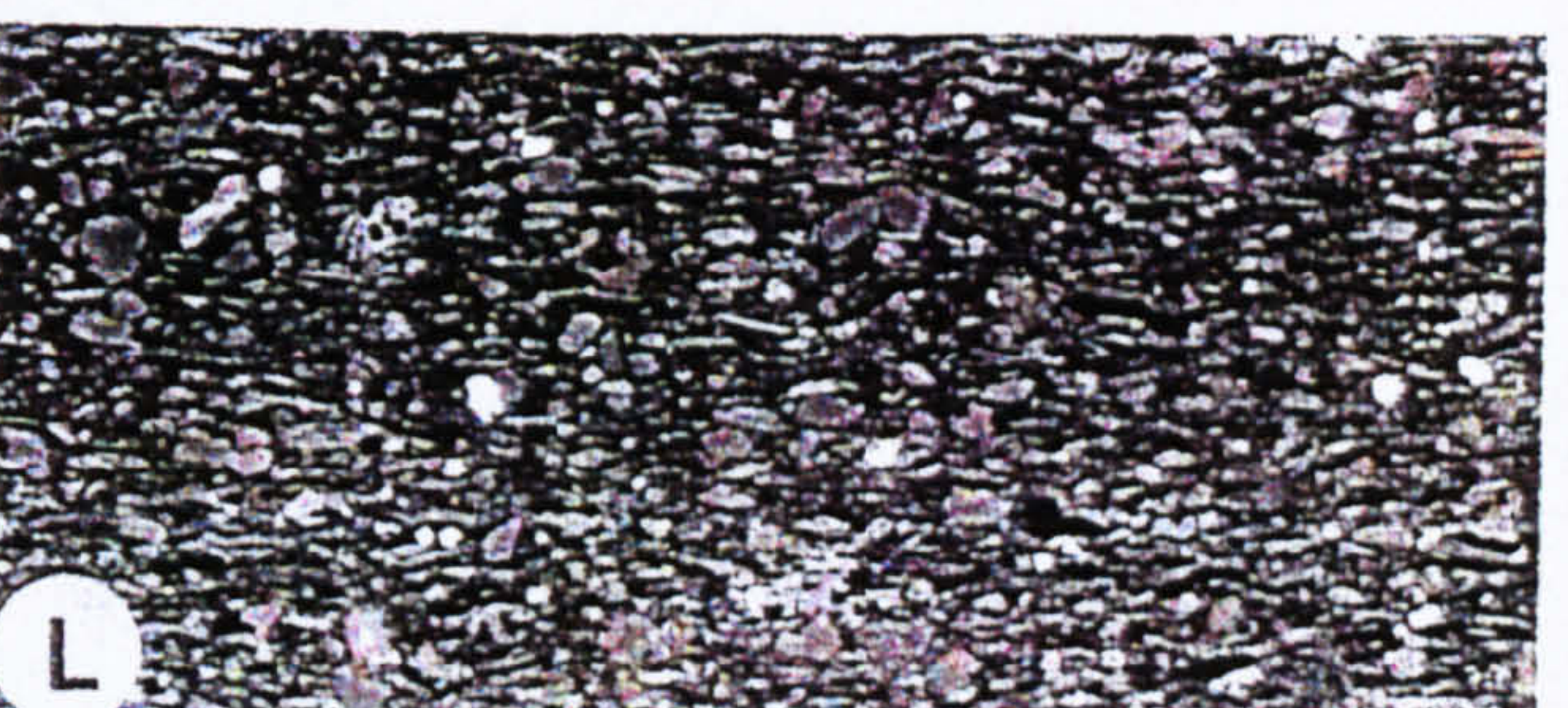
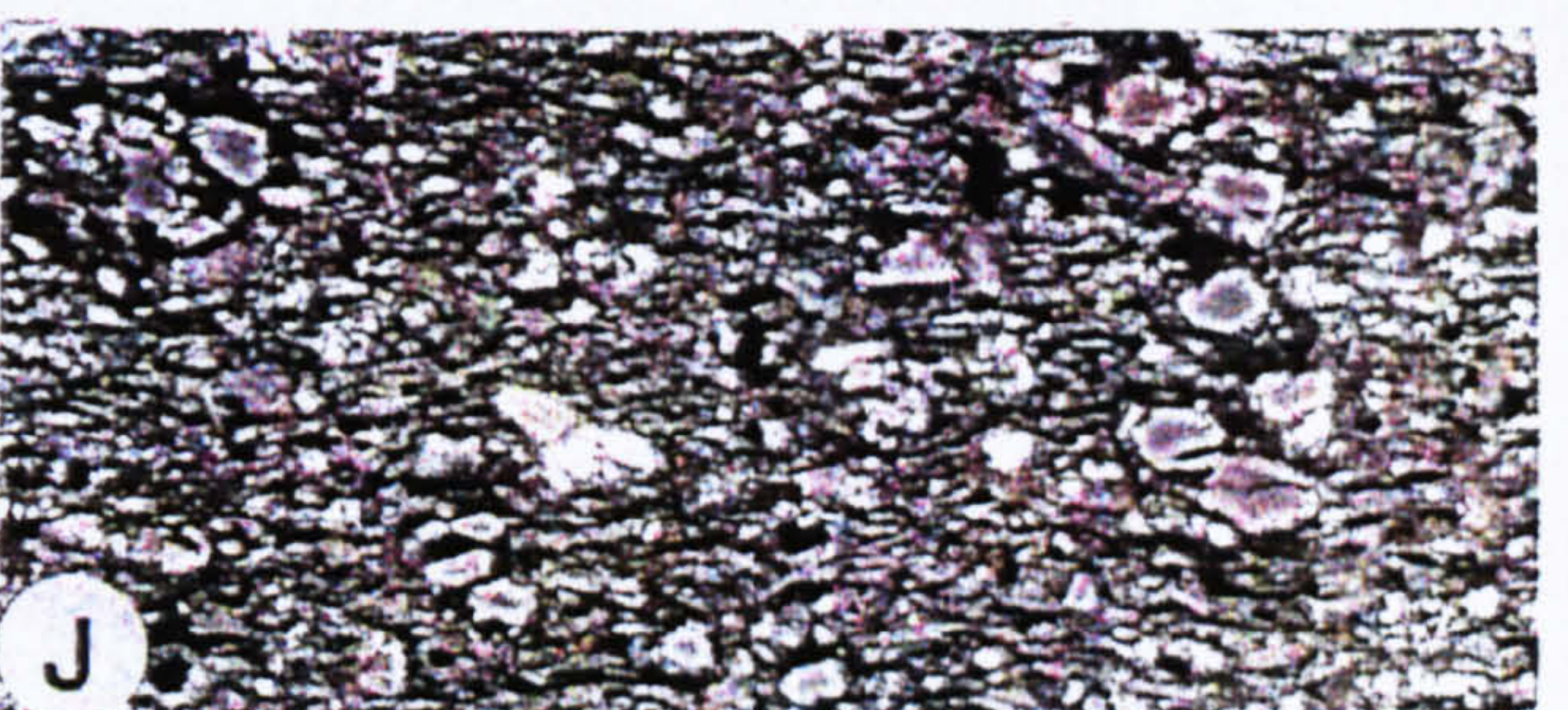
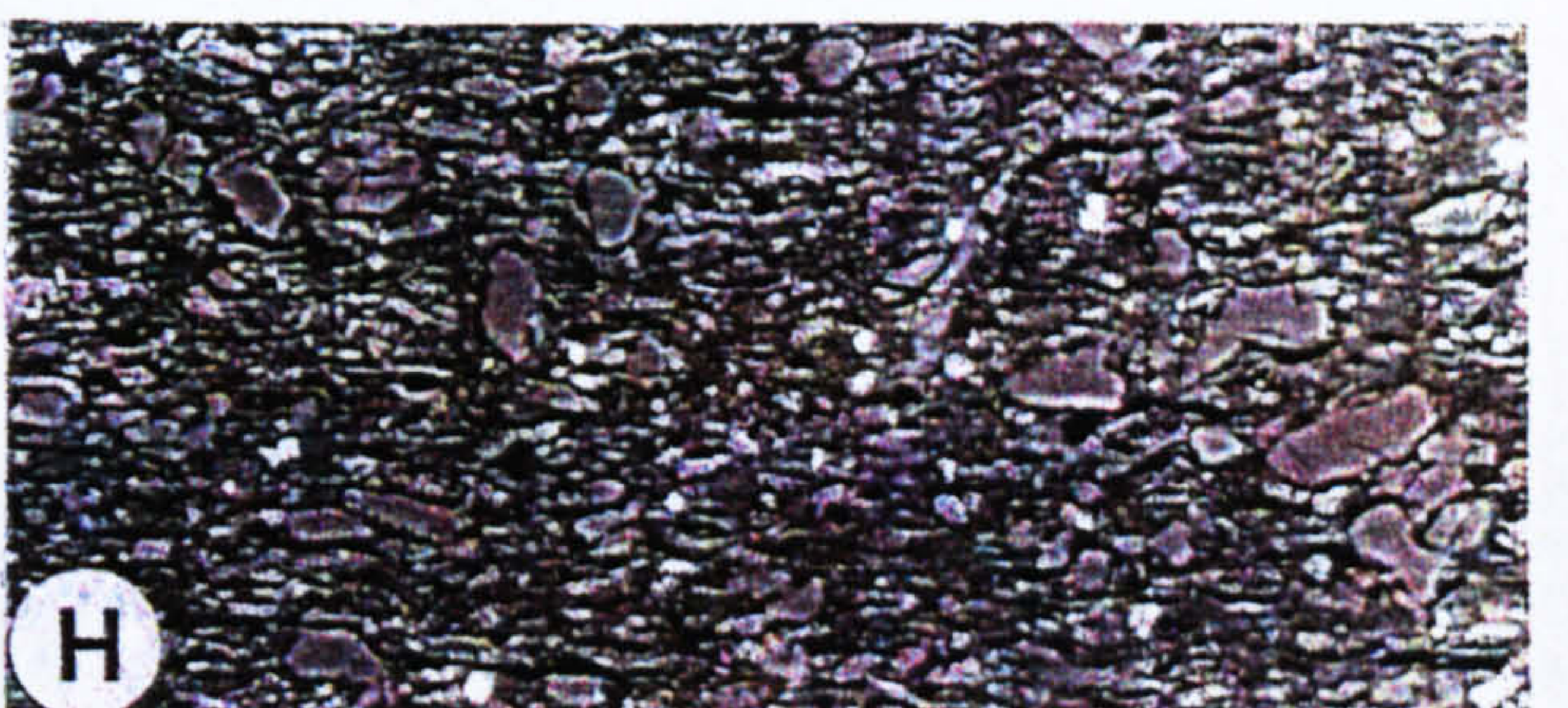
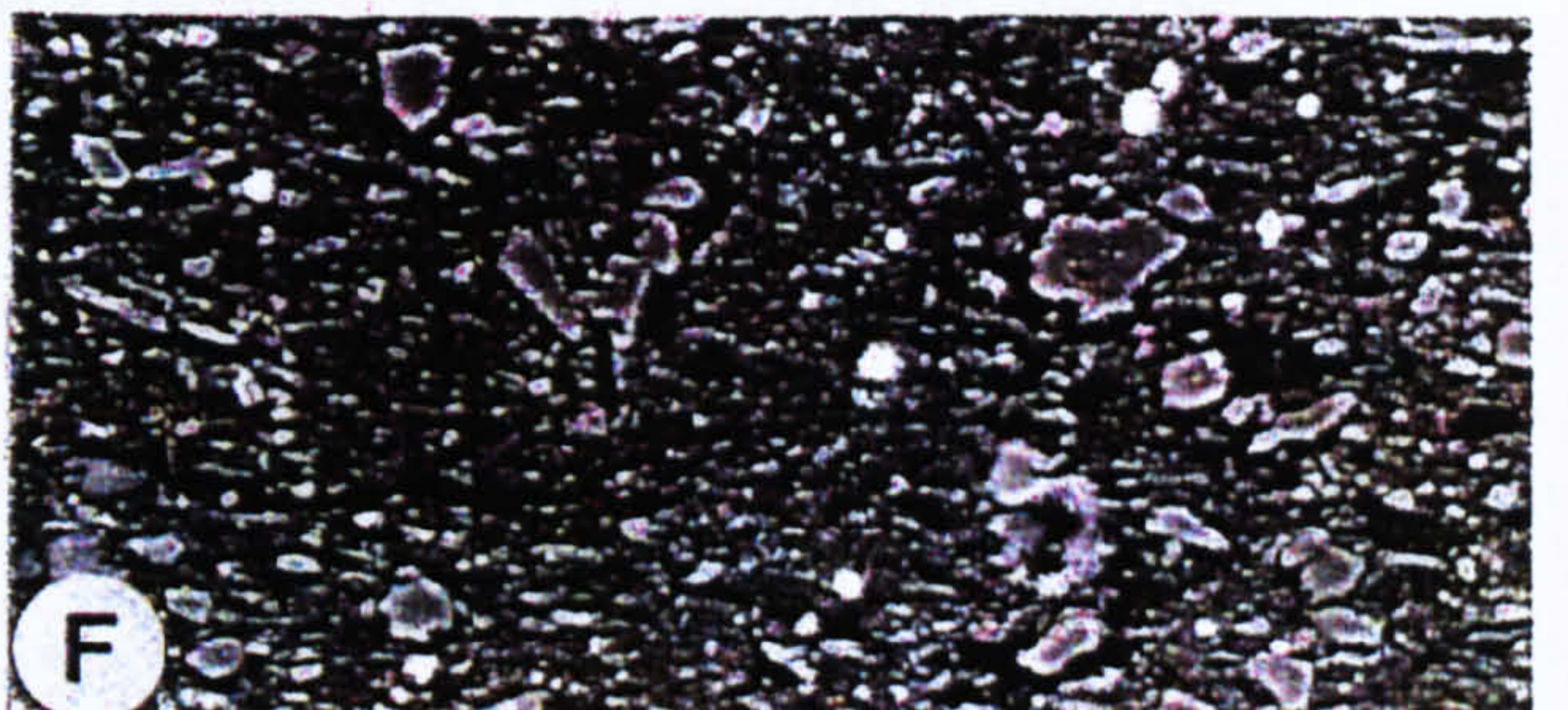
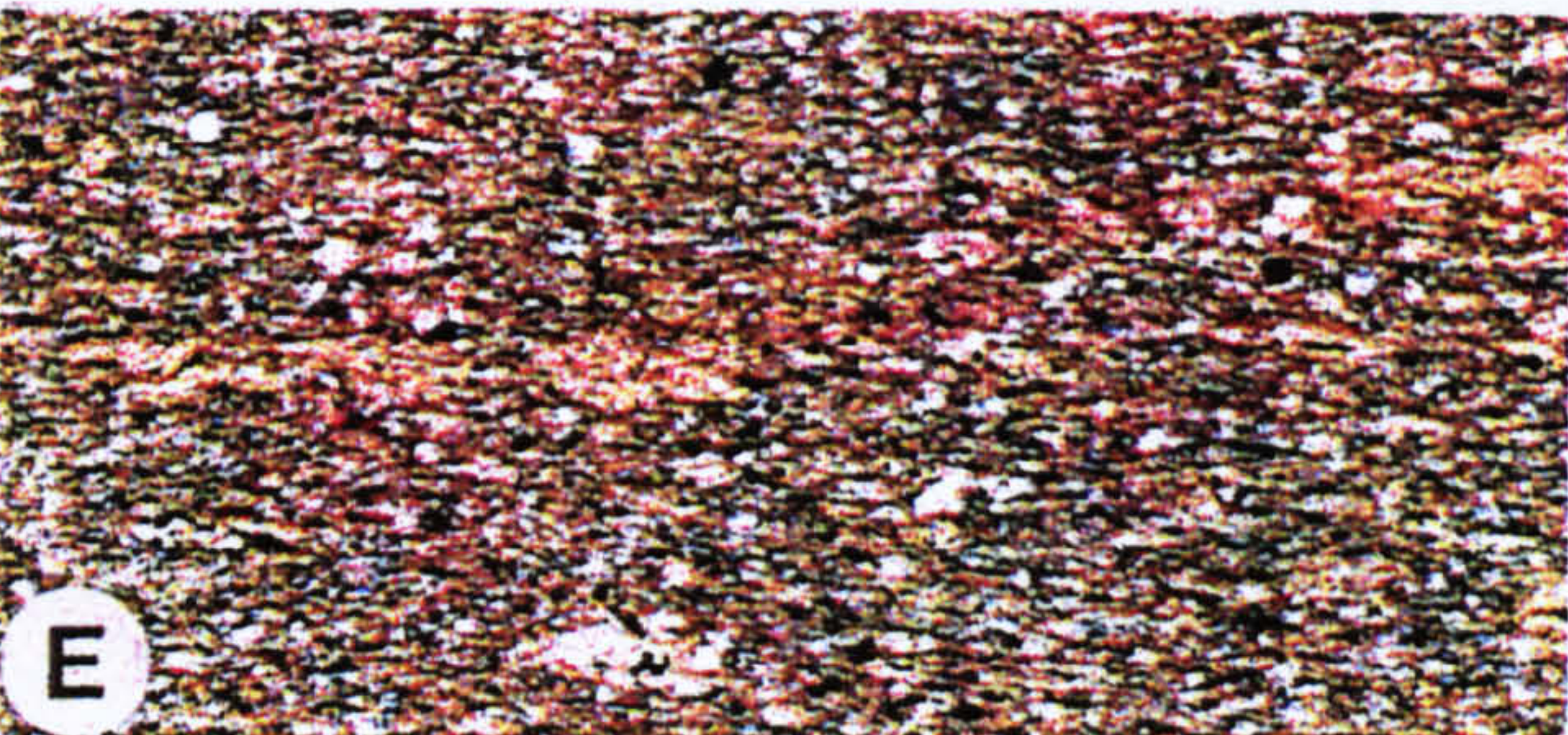
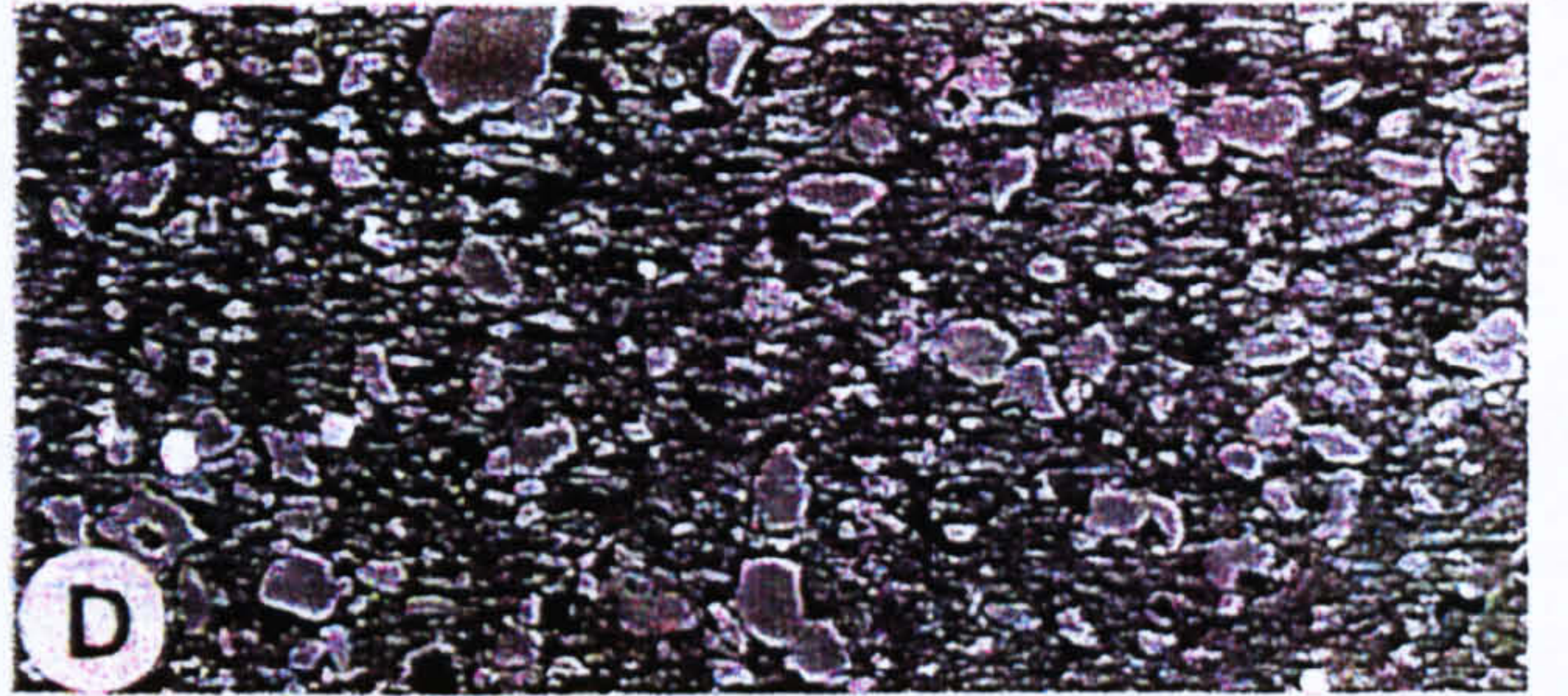
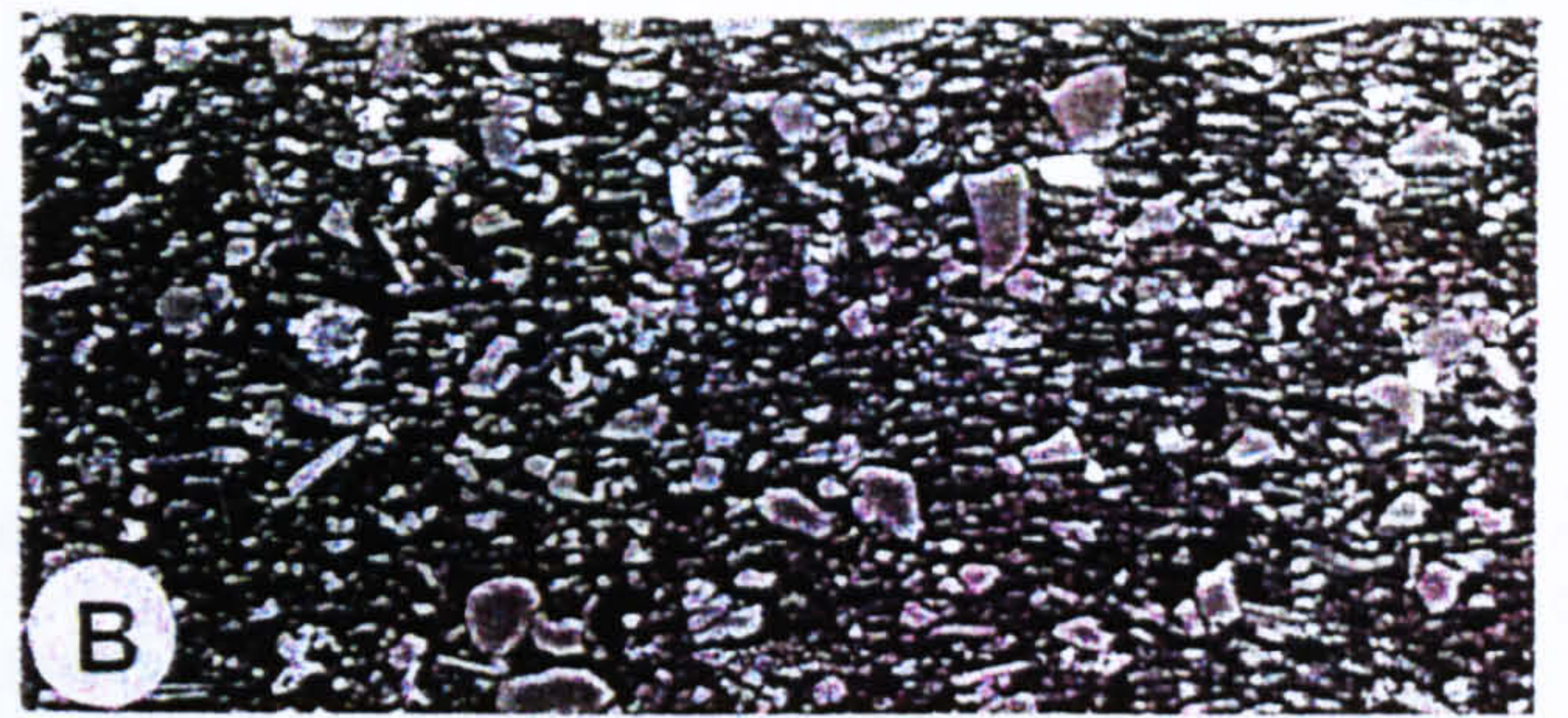
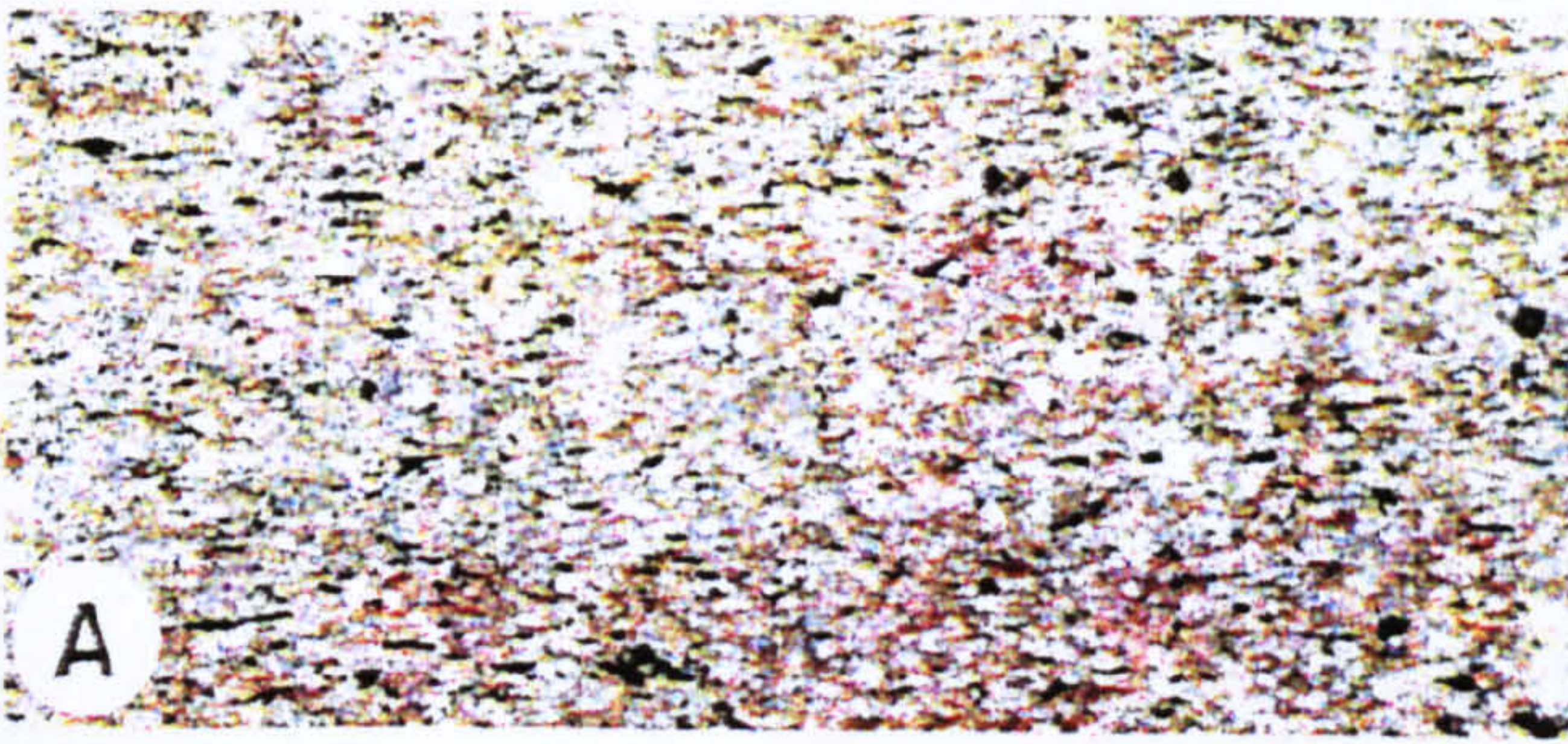


PLATE A4.8

Optical and BSE (backscattered electron) micrographs of vertical samples 0.07 to 0.33, Saxon pit (see Figure A4.1). Descriptions of the samples are given in Table A4.1.

- A optical micrograph of sample 0.33 (scale = x4); a silt-rich mudstone
- B BSE micrograph of sample 0.33 (scale = x250); a silt-rich mudstone
- C optical micrograph of sample 0.21 (scale = x4); a silt-rich mudstone
- D BSE micrograph of sample 0.21 (scale = x250); a silt-rich mudstone
- E optical micrograph of sample 0.07 (scale = x4); a silt-rich mudstone
- F BSE micrograph of sample 0.07 (scale = x250); a silt-rich mudstone

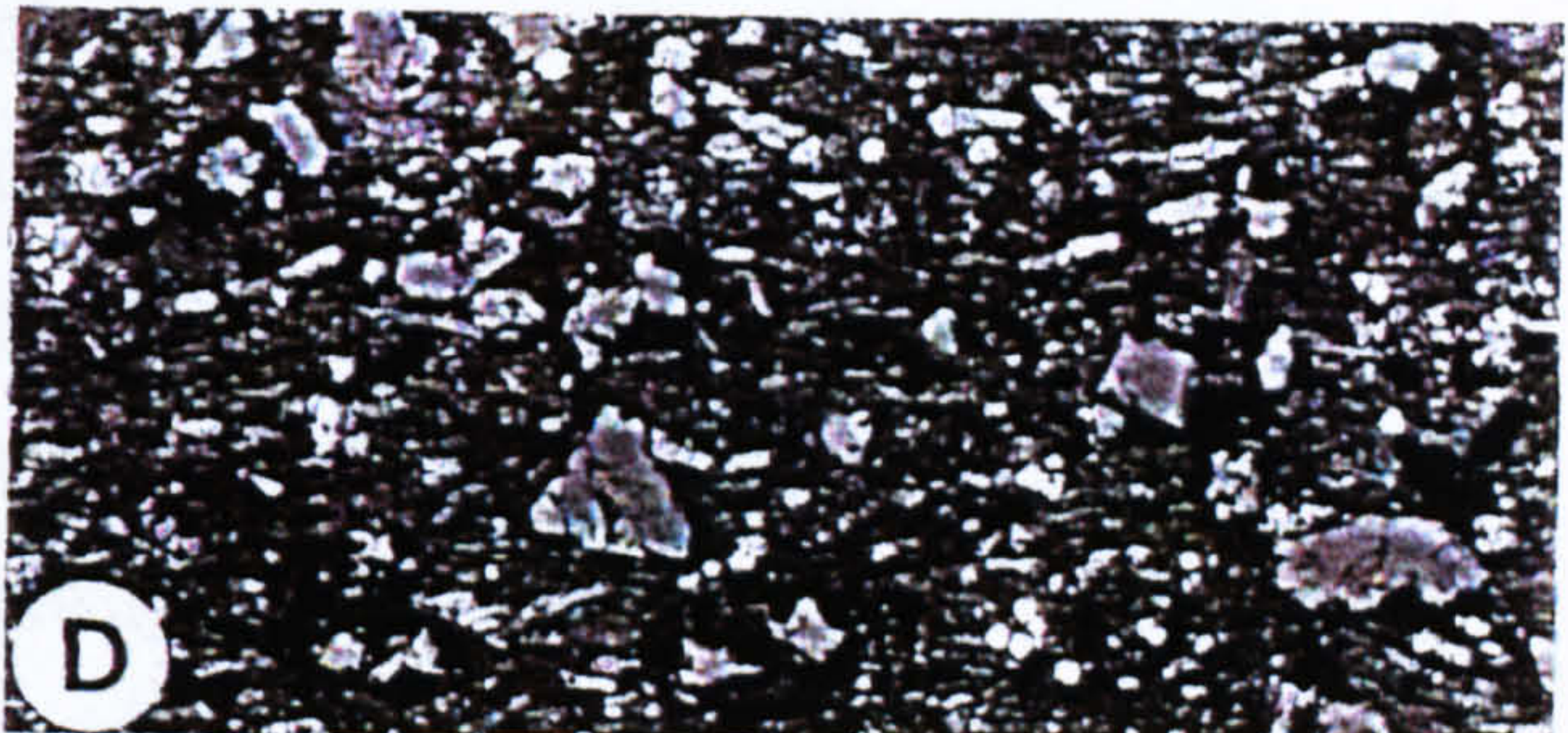
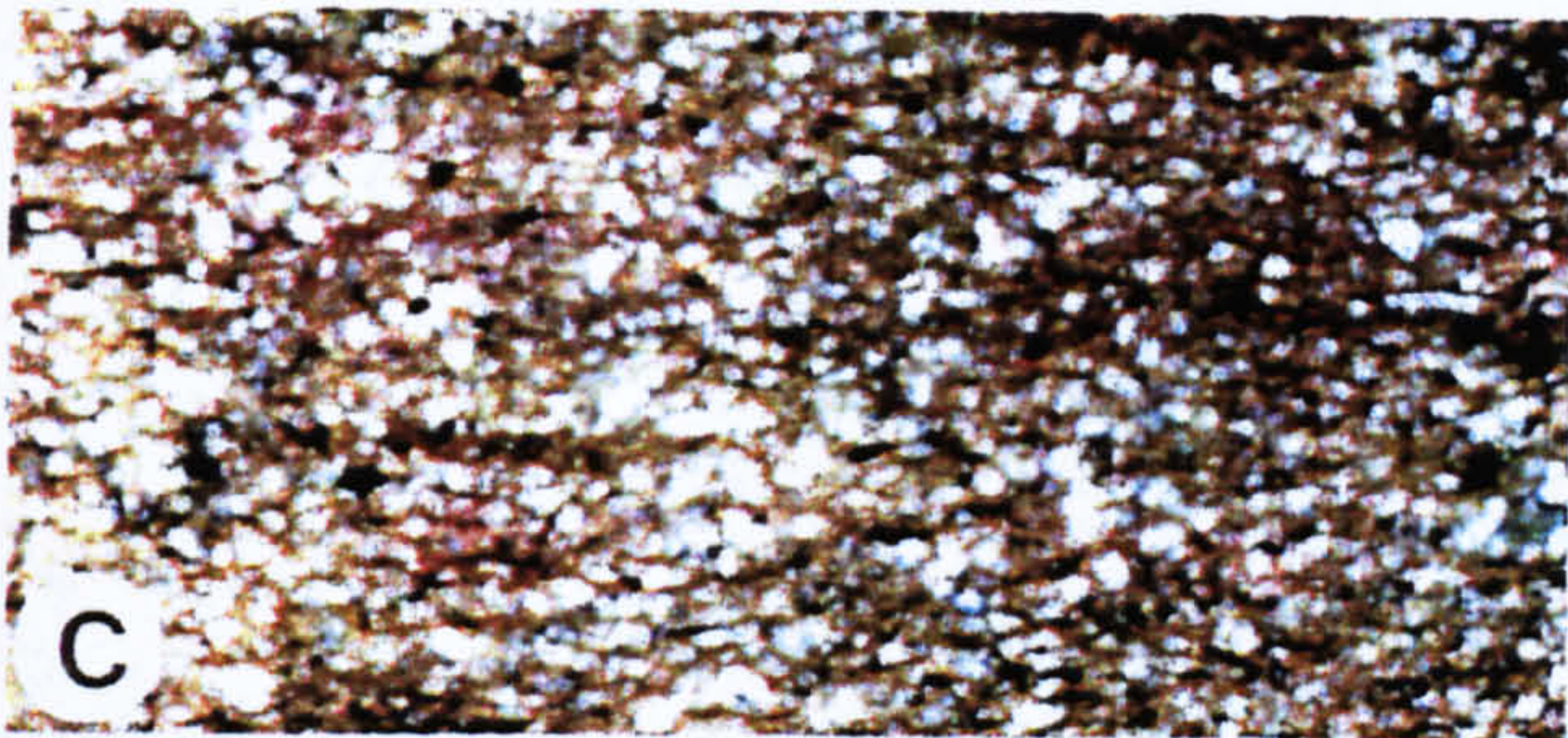
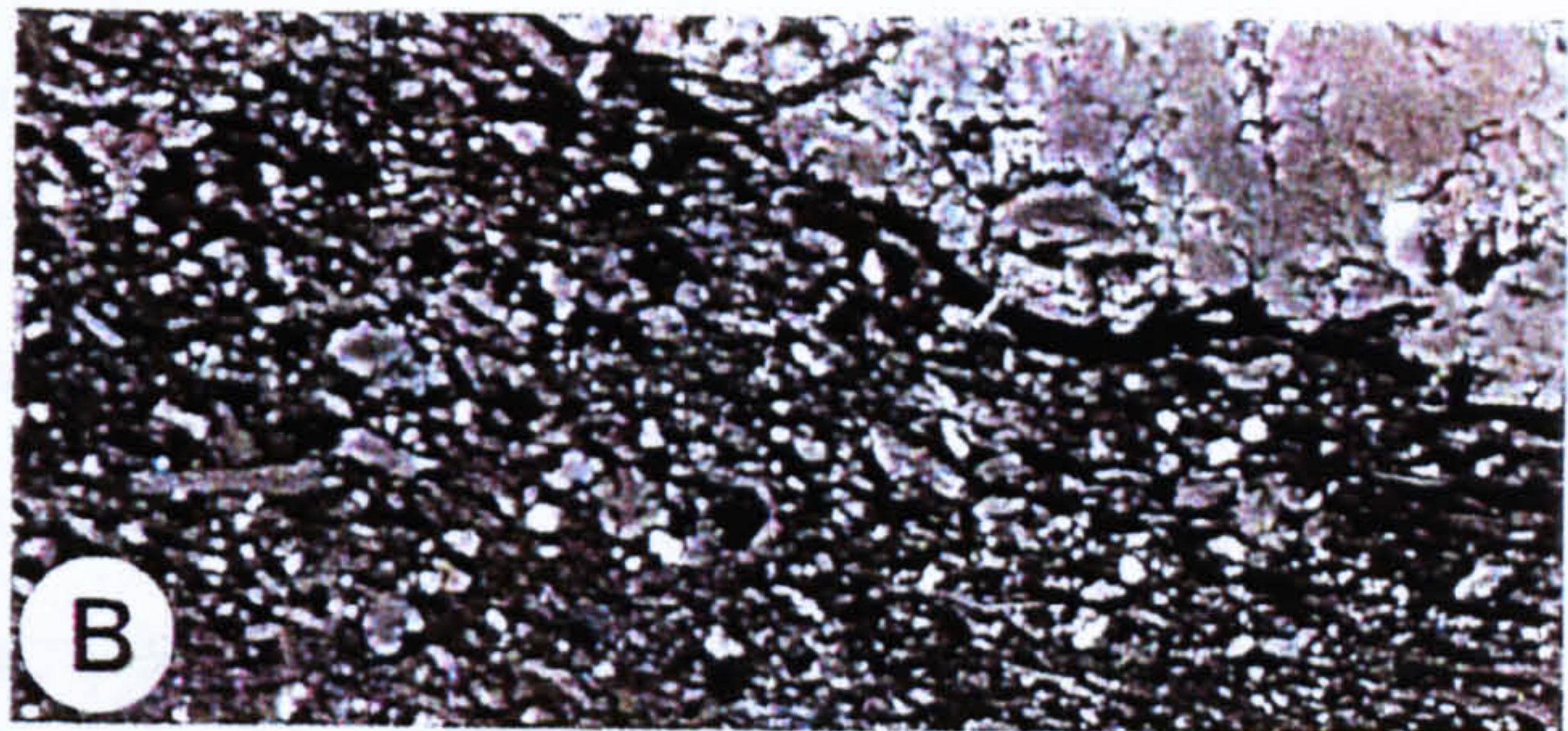
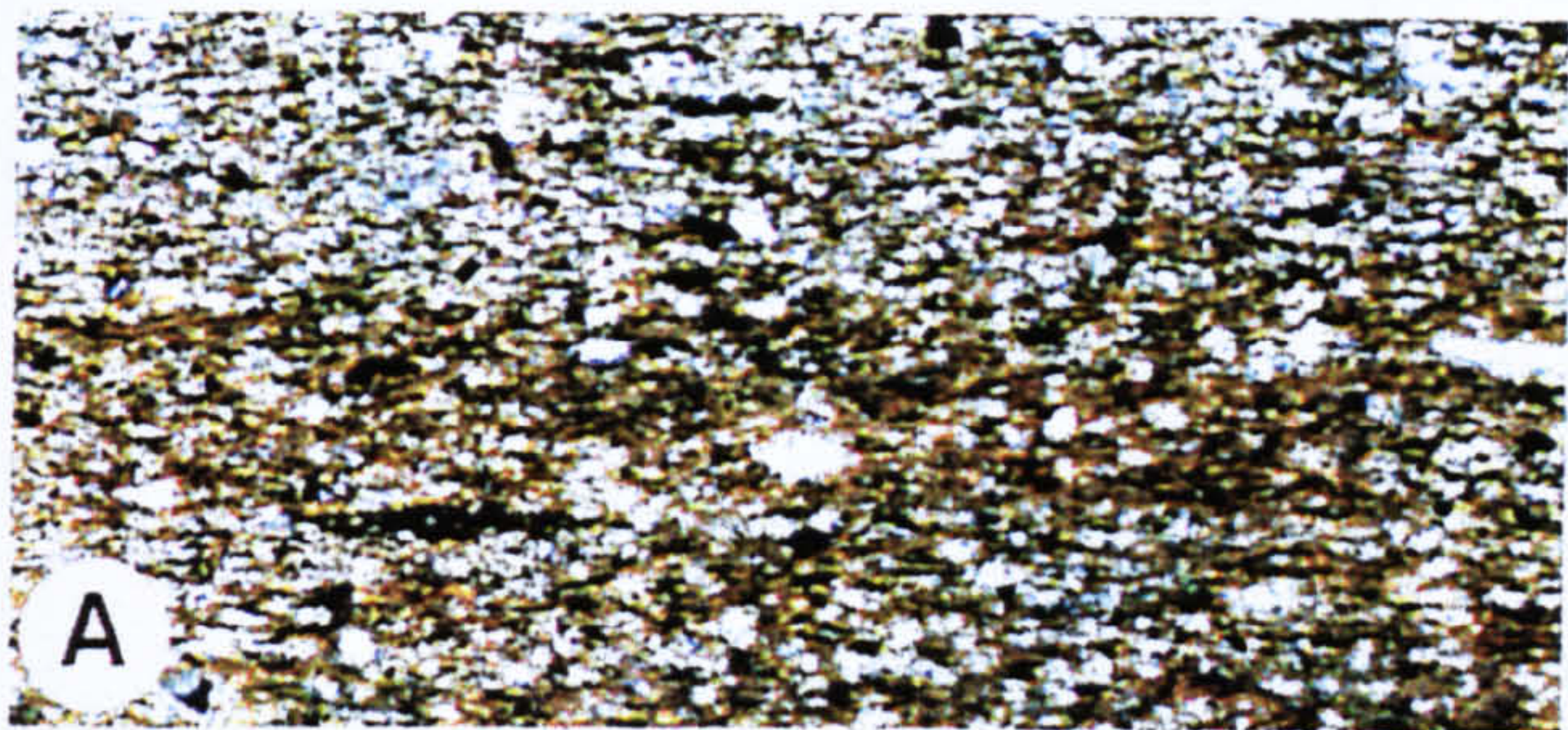


PLATE A4.9

Optical and BSE (backscattered electron) micrographs of lateral samples 1-6, Saxon pit. Descriptions of the samples are given in Table A4.1.

- A optical micrograph of lateral sample 1 (scale = x4); a silt-rich mudstone
- B BSE micrograph of lateral sample 1 (scale = x250); a silt-rich mudstone
- C optical micrograph of lateral sample 2 (scale = x4); a silt-rich mudstone
- D BSE micrograph of lateral sample 2 (scale = x250); a silt-rich mudstone
- E optical micrograph of lateral sample 3 (scale = x4); a silt-rich mudstone
- F BSE micrograph of lateral sample 3 (scale = x250); a silt-rich mudstone
- G optical micrograph of lateral sample 4 (scale = x4); a silt-rich mudstone
- H BSE micrograph of lateral sample 4 (scale = x250); a silt-rich mudstone
- I optical micrograph of lateral sample 5 (scale = x4); a silt-rich mudstone
- J BSE micrograph of lateral sample 5 (scale = x250); a silt-rich mudstone
- K optical micrograph of lateral sample 6 (scale = x4); a silt-rich mudstone
- L BSE micrograph of lateral sample 6 (scale = x250); a silt-rich mudstone

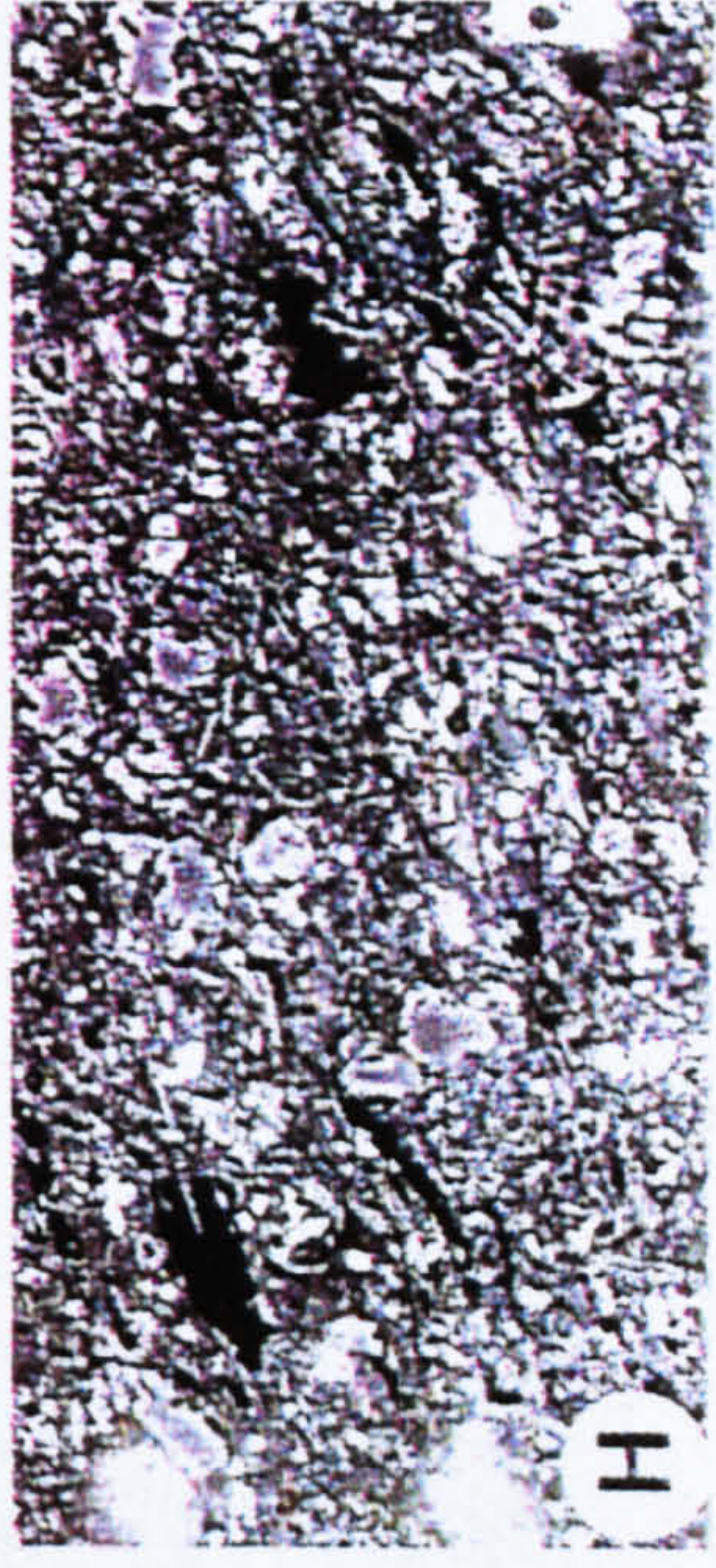
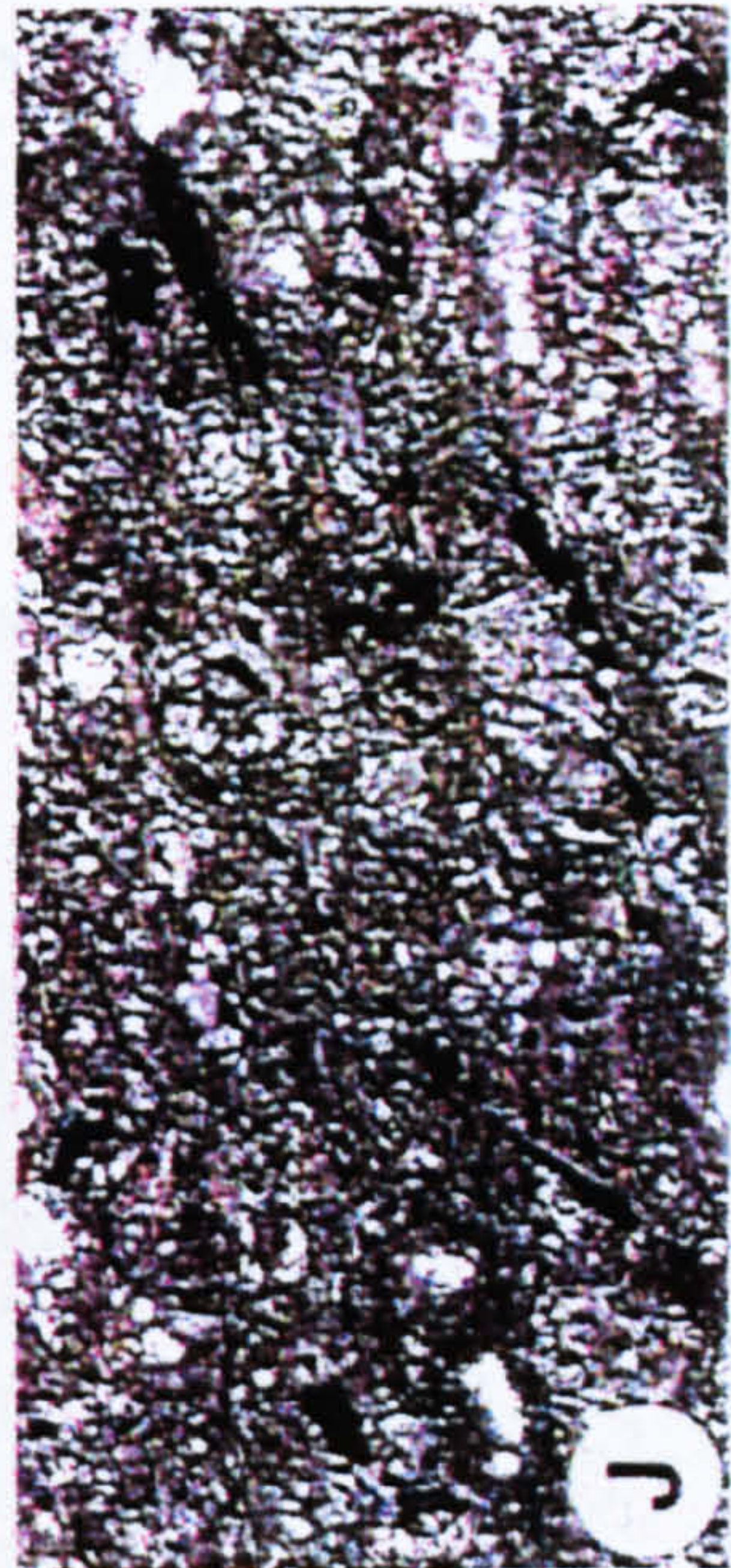
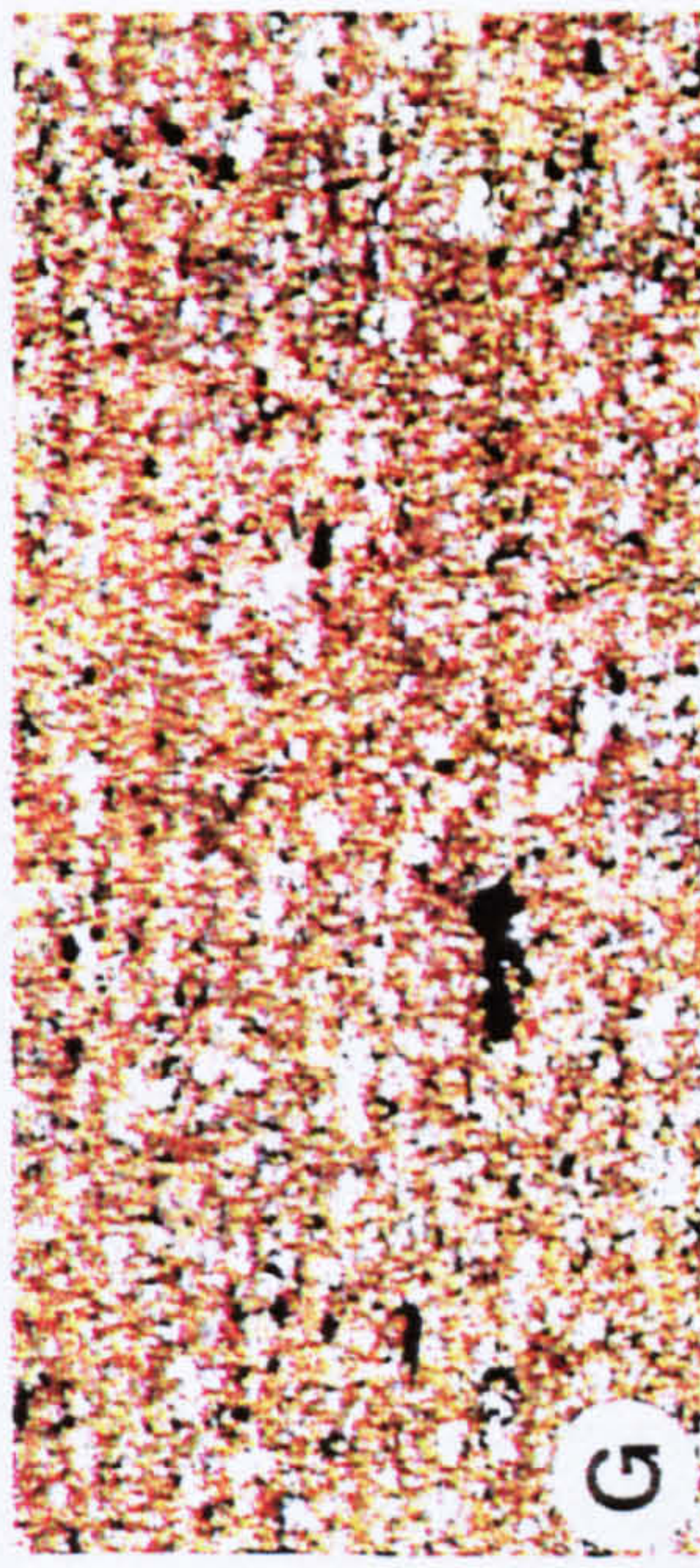
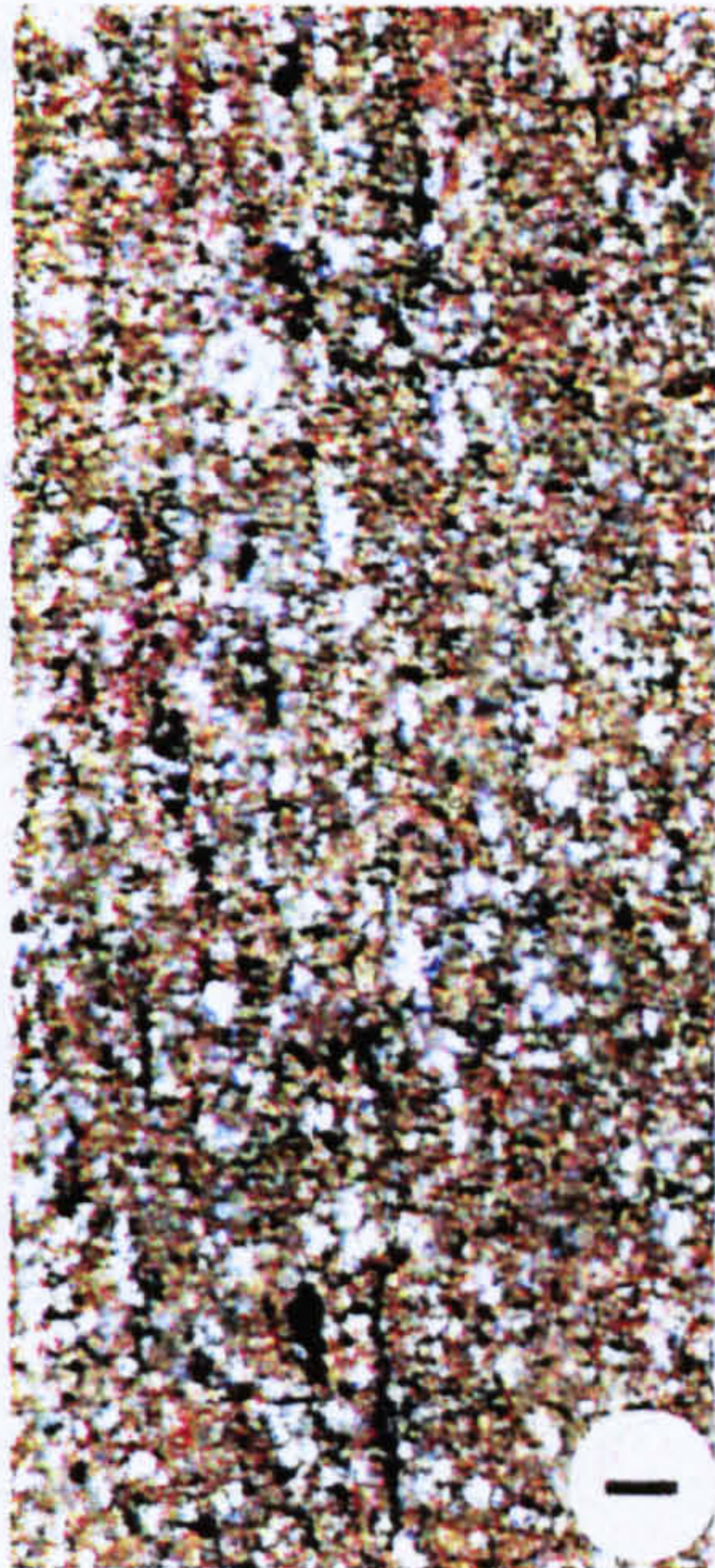
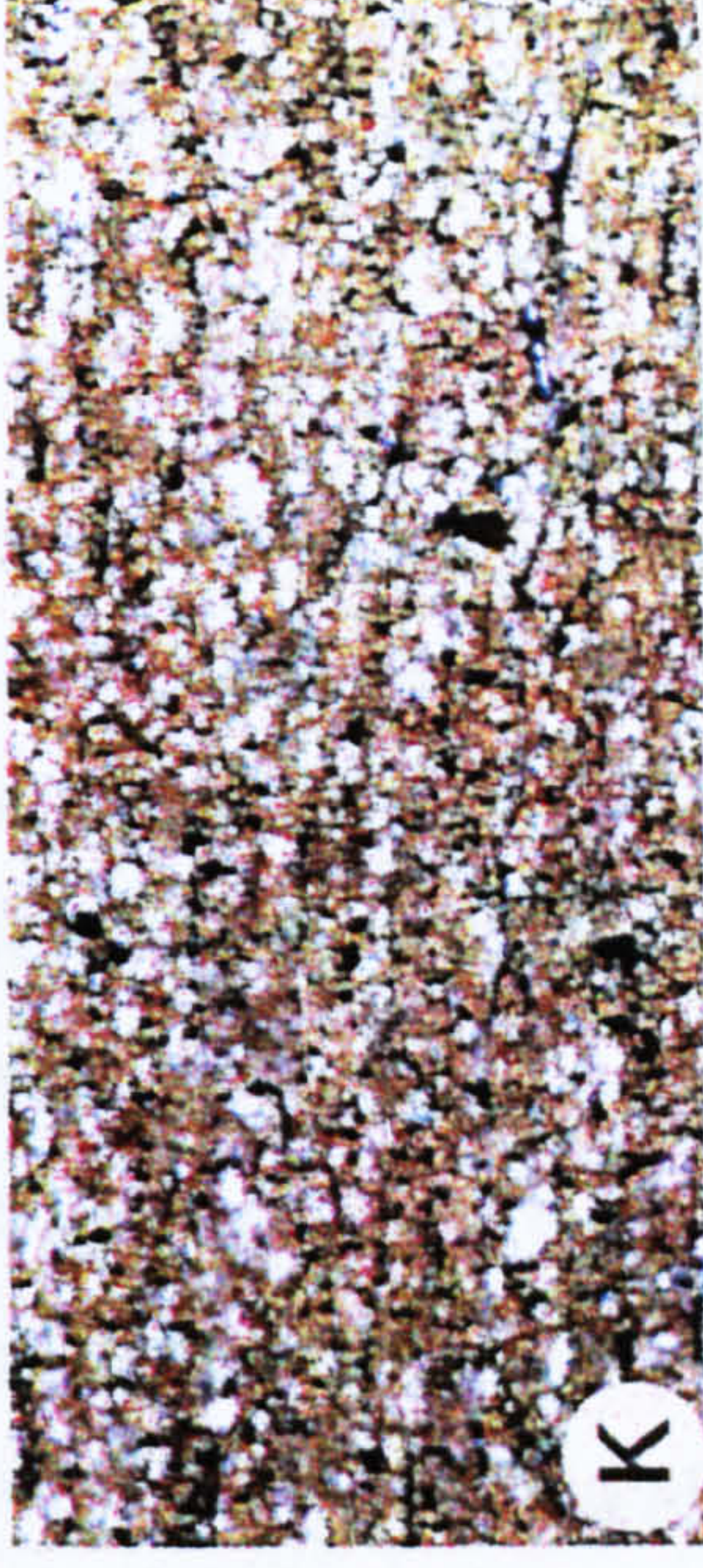
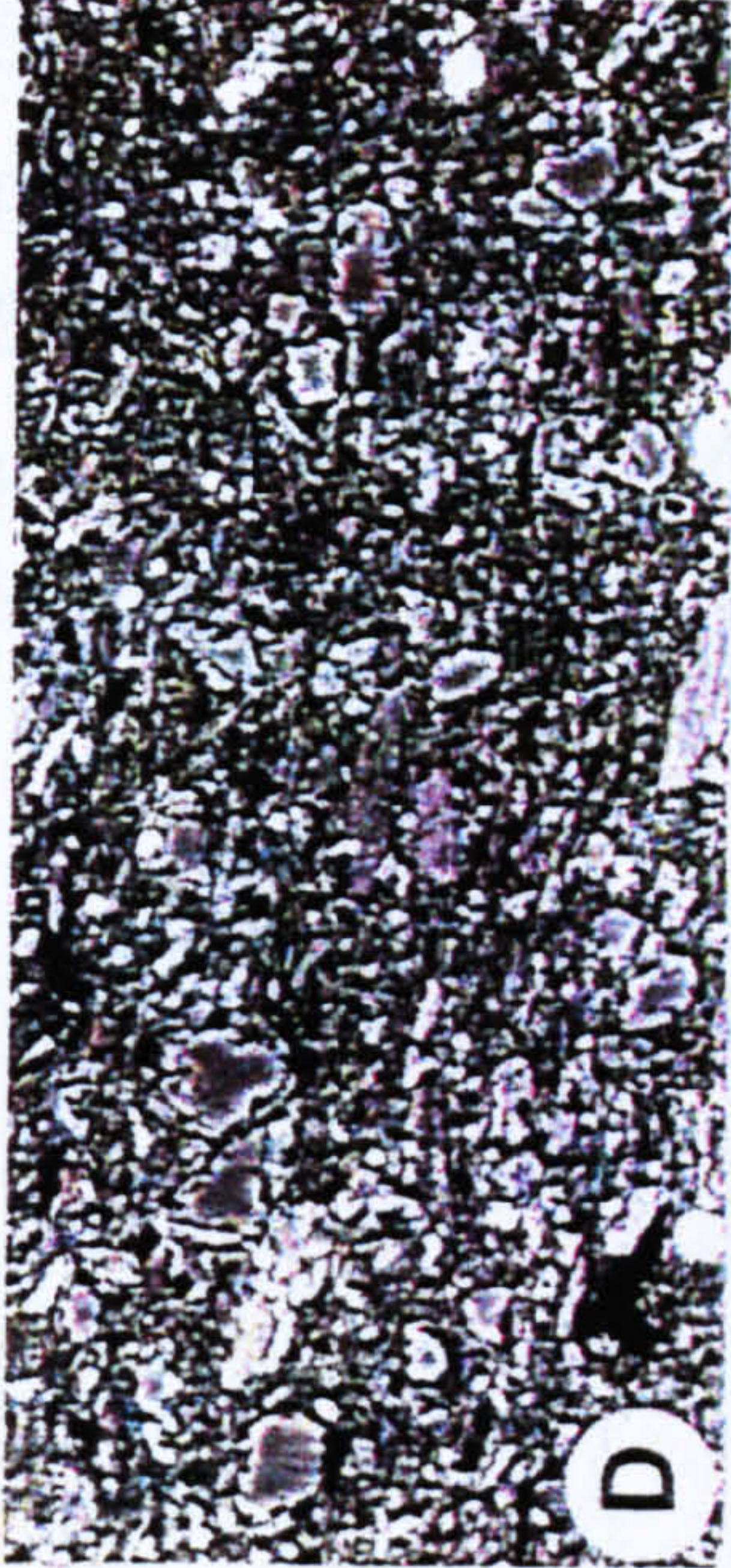
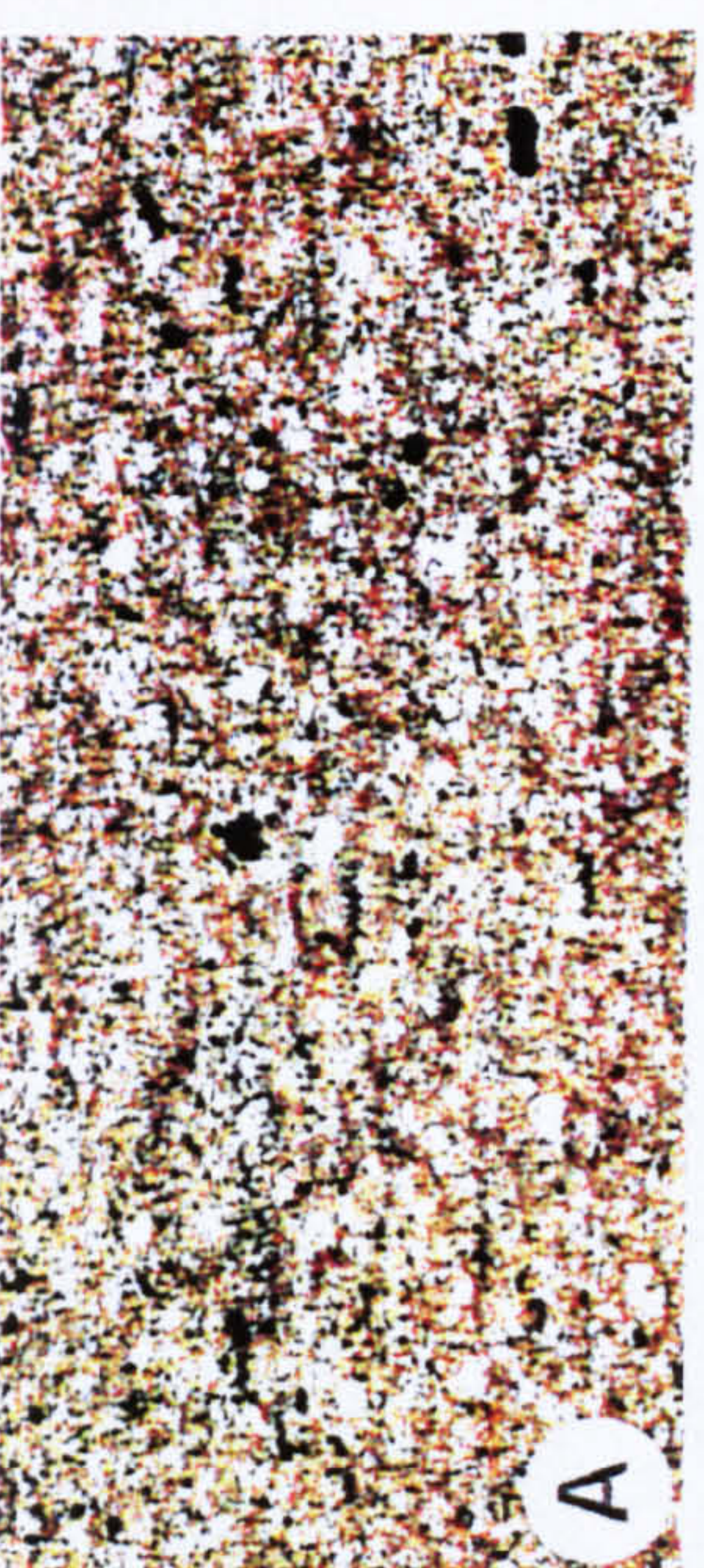
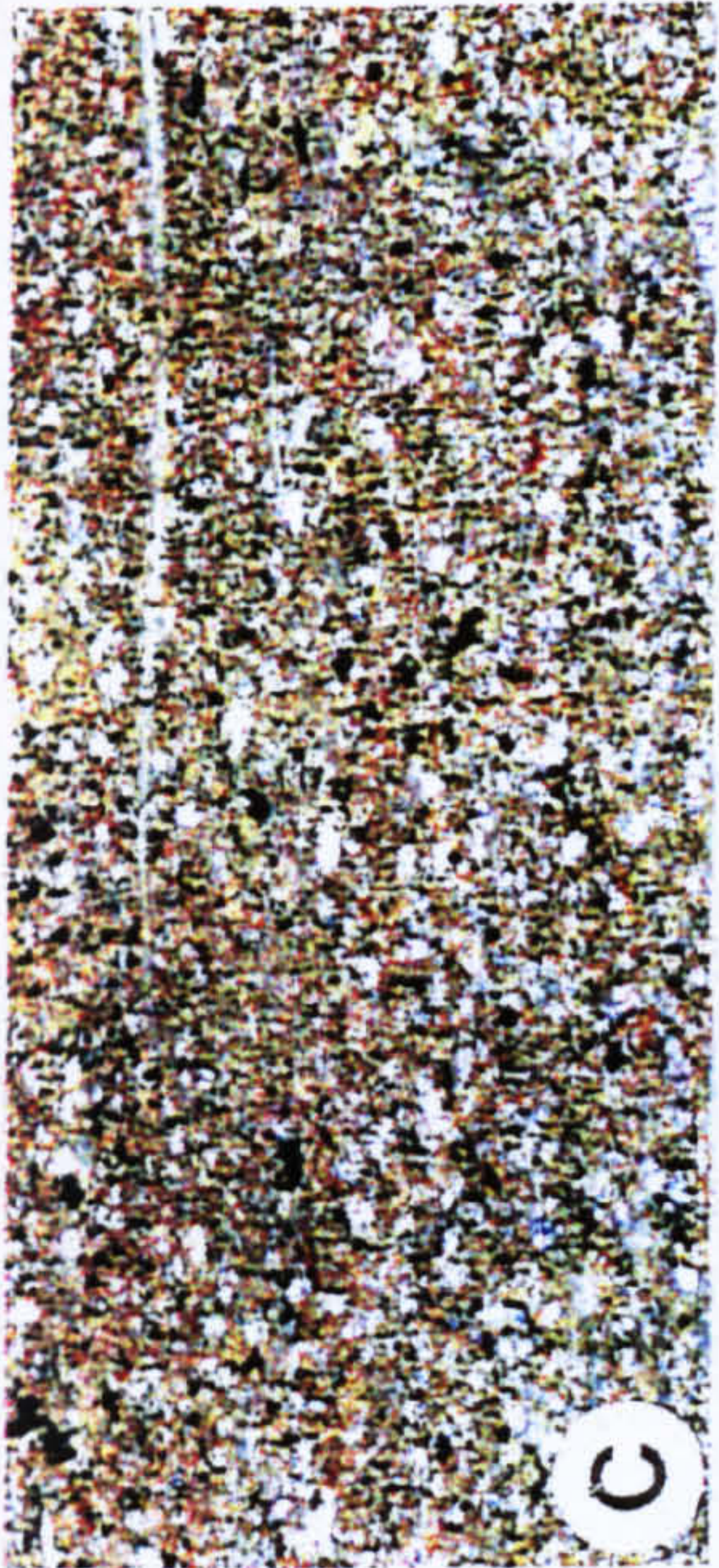
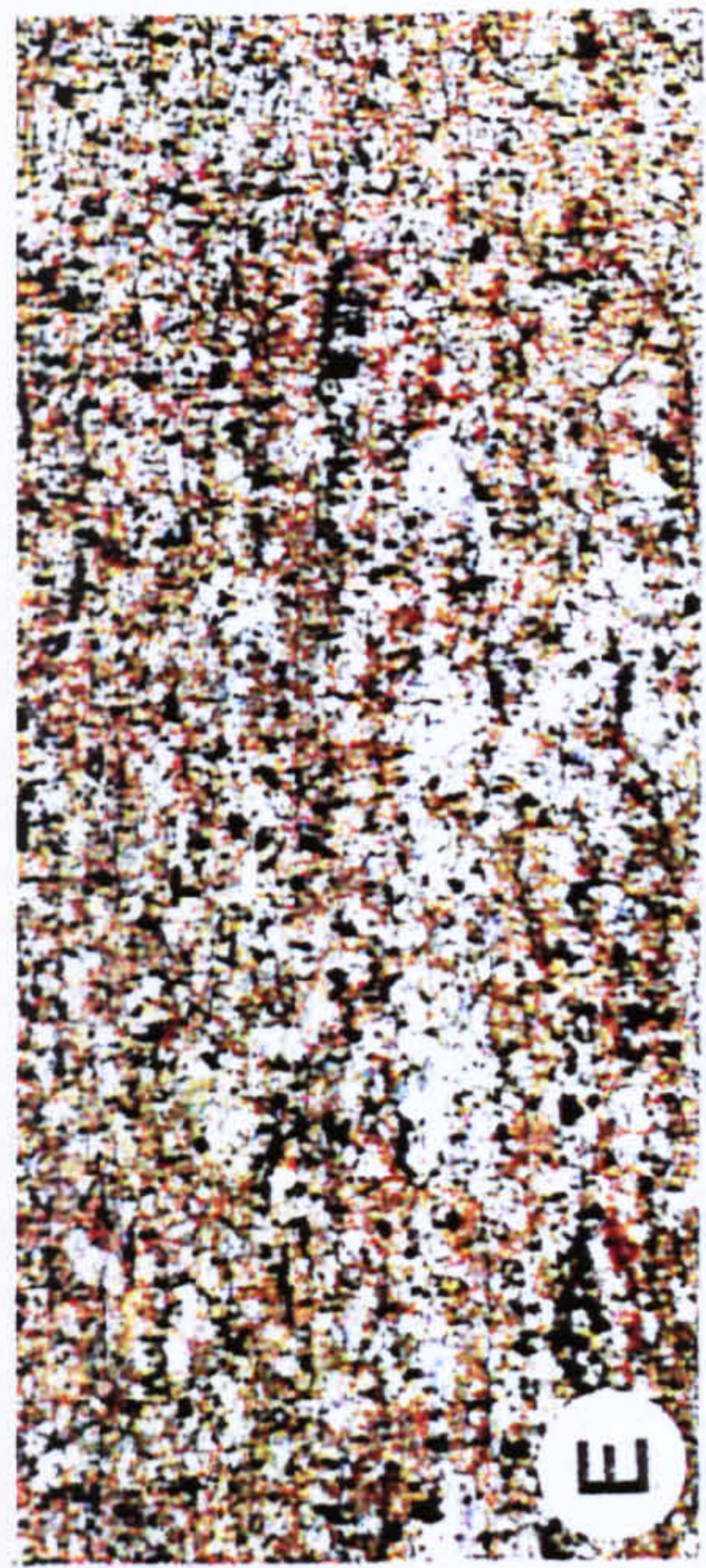


PLATE A4.10

Optical and BSE (backscattered electron) micrographs of lateral samples 7-12, Saxon pit. Descriptions of the samples are given in Table A4.1.

- A optical micrograph of lateral sample 7 (scale = x4); a silt-rich mudstone
- B BSE micrograph of lateral sample 7 (scale = x250); a silt-rich mudstone
- C optical micrograph of lateral sample 8 (scale = x4); a silt-rich mudstone
- D BSE micrograph of lateral sample (scale = x250); a silt-rich mudstone
- E optical micrograph of lateral sample 9 (scale = x4); a silt-rich mudstone
- F BSE micrograph of lateral sample 9 (scale = x250); a silt-rich mudstone
- G optical micrograph of lateral sample 10 (scale = x4); a silt-rich mudstone
- H BSE micrograph of lateral sample 10 (scale = x250); a silt-rich mudstone
- I optical micrograph of lateral sample 11 (scale = x4); a silt-rich mudstone
- J BSE micrograph of lateral sample 11 (scale = x250); a silt-rich mudstone
- K optical micrograph of lateral sample 12 (scale = x4); a silt-rich mudstone
- L BSE micrograph of lateral sample 12 (scale = x250); a silt-rich mudstone

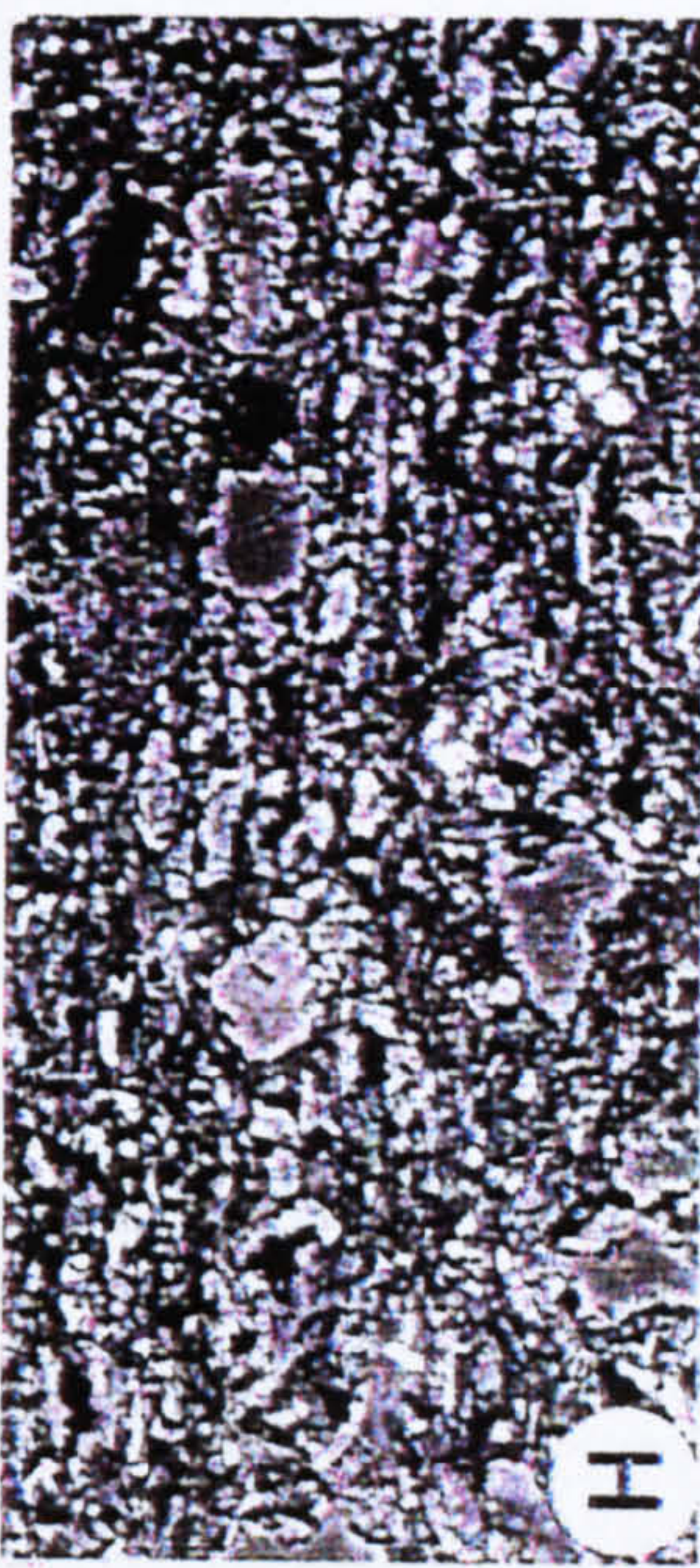
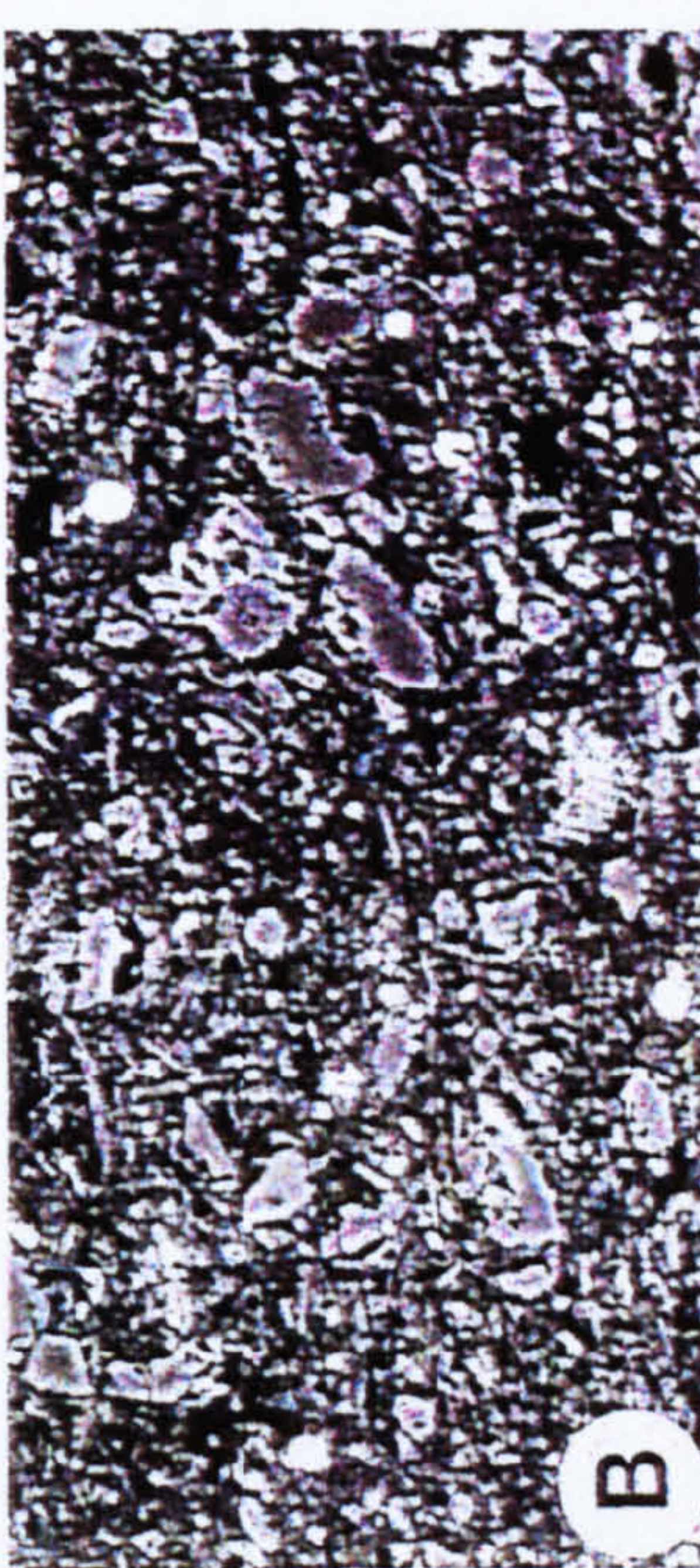
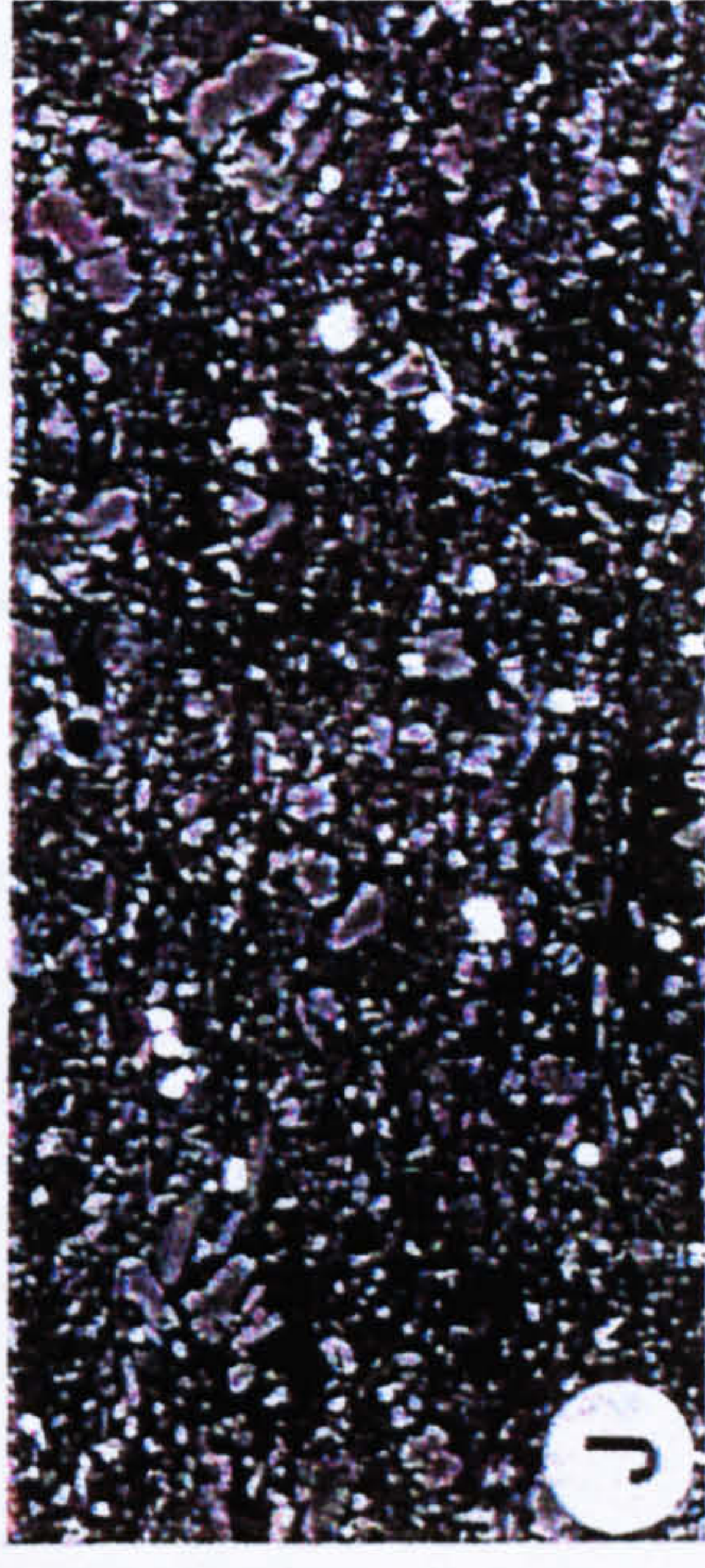
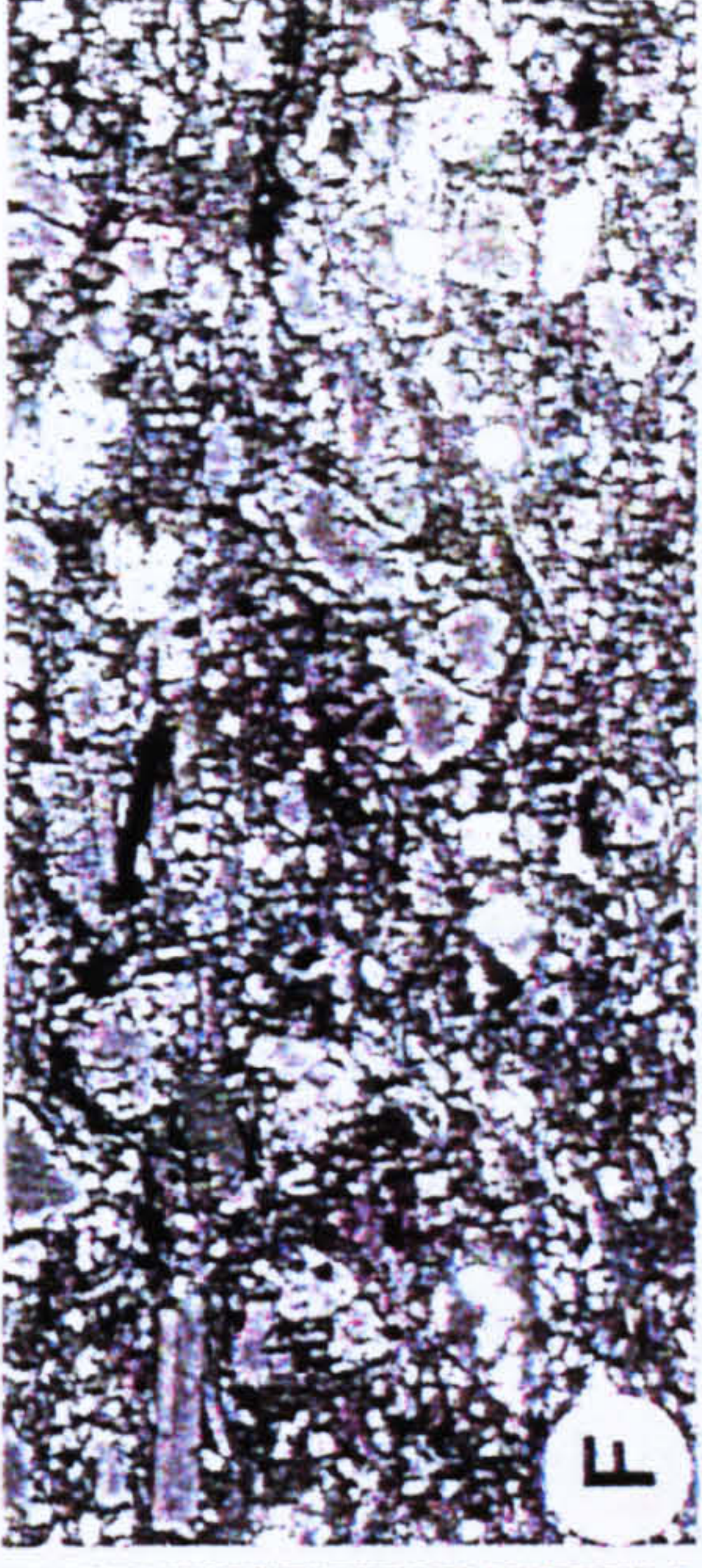
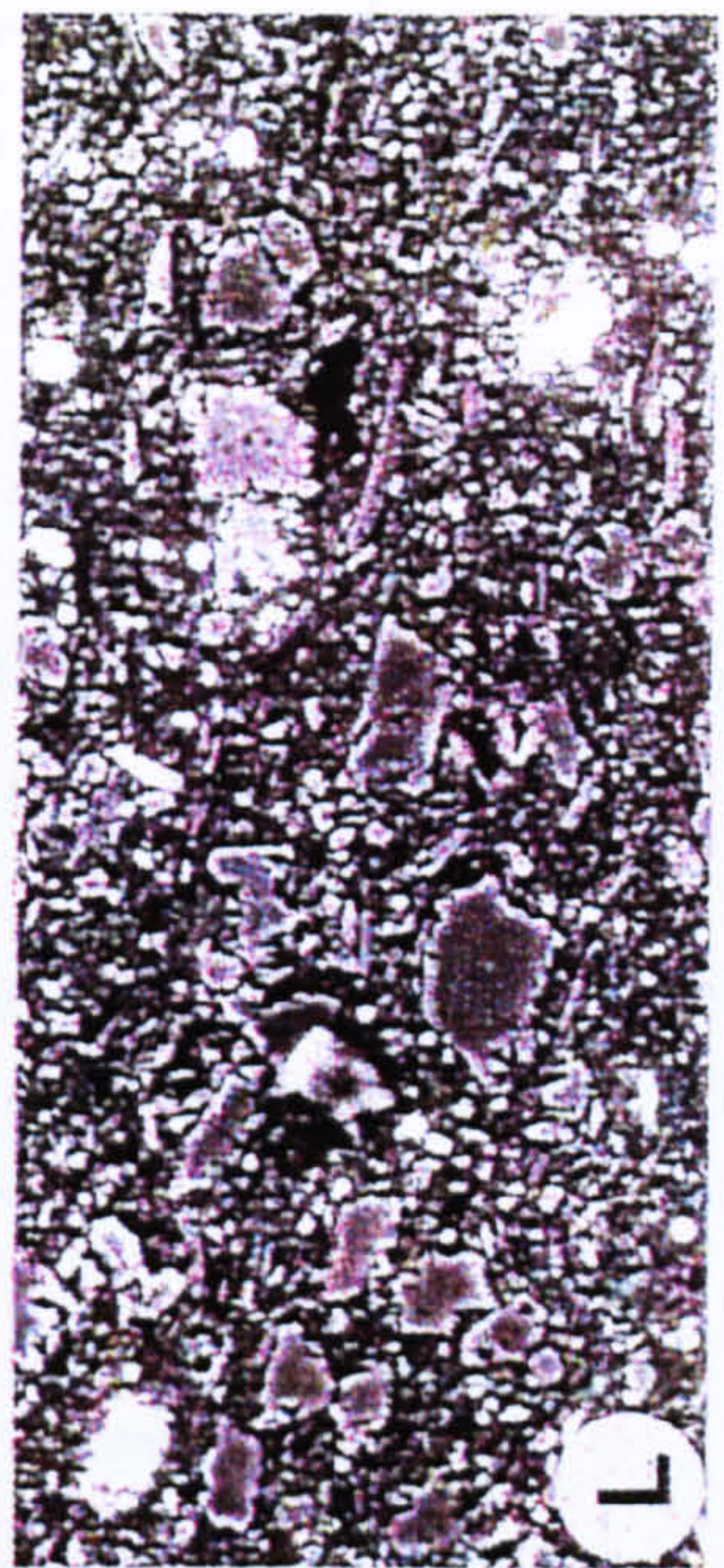


PLATE A4.11

Optical and BSE (backscattered electron) micrographs of lateral samples 13-18; lateral samples 13-15 are from Saxon pit, lateral samples 16-18 are from King's Dyke pit (grid reference TL 248 967). Descriptions of the samples are given in Table A4.1.

- A optical micrograph of lateral sample 13 (scale = x4); a silt-rich mudstone
- B BSE micrograph of lateral sample 13 (scale = x250); a silt-rich mudstone
- C optical micrograph of lateral sample 14 (scale = x4); a clay-rich mudstone
- D BSE micrograph of lateral sample 14 (scale = x250); a clay-rich mudstone
- E optical micrograph of lateral sample 15 (scale = x4); a silt-rich mudstone
- F BSE micrograph of lateral sample 15 (scale = x250); a silt-rich mudstone
- G optical micrograph of lateral sample 16 (scale = x4); a silt-rich mudstone
- H BSE micrograph of lateral sample 16 (scale = x250); a silt-rich mudstone
- I optical micrograph of lateral sample 17 (scale = x4); a silt-rich mudstone
- J BSE micrograph of lateral sample 17 (scale = x250); a silt-rich mudstone
- K optical micrograph of lateral sample 18 (scale = x4); a silt-rich mudstone
- L BSE micrograph of lateral sample 18 (scale = x250); a silt-rich mudstone



Small-scale (≤ 5.0 m) vertical heterogeneity in mudstones: implications for high-resolution stratigraphy in siliciclastic mudstone successions

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Abstract: 48 mudstone samples, from the Peterborough Member, Oxford Clay Formation, have been analysed to determine the small-scale vertical and lateral lithofacies variability in this succession. The samples were collected every 0.15 m from Saxon and King's Dyke brickpits (Whittlesey, Peterborough, UK) over a short vertical interval (15 m). The sampled interval spans the *obductum* to the *grossouvrei* Subzones of the Callovian (Upper Jurassic). Lithofacies present were described using combined field logging, optical and backscattered electron optical techniques.

The succession predominantly comprises silt-rich mudstones, with subordinate clay-rich mudstones, shell-beds and shell-pavements. The individual units are variously composed of detrital clay, quartz, pyrite, calcite with minor apatite, kaolinite and glauconite. In some units millimetre-scale upward-fining couplets are present; elsewhere, the original bedding structures have been destroyed by bioturbation. Comparison of successive thin sections reveals that upward-coarsening is present on a metre-scale and that shell-enriched units are located close to the tops of these upward-shoaling units. Comparison of samples collected laterally on a 0.01–1.0 m scale from the same level (3.0 m below the top of Bed 14) indicates that there is lateral lithofacies variability.

The small-scale (0.001 m) couplets are interpreted to be beds having been deposited by waning flow currents. Significant breaks between these depositional events allowed a dysaerobic infauna to colonize the sediment. The metre-scale upward-coarsening intervals which are capped by shell-enriched units are interpreted to be parasequences.

The observed small-scale lateral lithofacies variability is interpreted to be a product of small, but significant vertical miscorrelation errors rather than systematic lateral facies changes. These data suggest that producing reliable, bed-scale lateral correlations over distances of more than 1 km in this, and successions like it, will be very difficult.

Keywords:

Historically, geologists have commonly assumed that the variability present within siliciclastic mudstone (shale) units mainly records changes in primary productivity and bottom water anoxia (e.g. Pedersen & Calvert 1990) as opposed to changes in detrital sediment input. This paradigm, combined with classical stratigraphic methods has led many workers (e.g. Cox & Gallois 1981) to argue that some beds can be correlated over large areas within individual basins. These factors, coupled with the fact that mudstone successions commonly contain the most complete stratigraphic record, has led some stratigraphers to intensively investigate these sediments as repositories of high-resolution stratigraphical data. These latter studies have commonly aimed to provide a detailed record of environmental change leading to the ultimate goal of dramatically refining stratigraphical correlations.

Recent work (e.g. Macquaker & Gawthorpe 1993; Macquaker 1994; Macquaker & Taylor 1996; Macquaker *et al.* in press) demonstrates that there is significant lateral and vertical lithofacies variability within mudstone successions particularly in terms of their clastic components. Moreover, they along with other workers (e.g. Leithold 1994; Wignall 1991, 1994; Schwalbach & Bohacs 1992; Curiale *et al.* 1991; Creaney & Passey 1993; Pasley 1991; Isaksen & Bohacs 1994; Leckie *et al.* 1990) utilizing different techniques (such as sieving, wireline logs and gas chromatography, mass-spectrometry, etc.) have shown that this variability is system-

atic and can be interpreted within a sequence stratigraphic framework. While these workers have variously demonstrated parasequence (commonly 0.1–1.0 m) and systems tract (commonly 1.0–10.0 m) scale variability, they have largely ignored small-scale (< 0.1 m) heterogeneity. This omission is crucial because it is at this scale that high-resolution stratigraphers aim to correlate between sections around sedimentary basins.

Detailed work on some mudstone successions (e.g. Cleveland Ironstone Formation, Lower Jurassic, Yorkshire, UK, Macquaker & Taylor 1997) has demonstrated that units described as 'beds' for stratigraphic convenience on the basis of field investigations (for example Howard 1985; Callomon 1968; Duff 1975; Hudson & Martill 1994) are actually recording stratigraphic information at either a bed-set, parasequence or greater scale. In these successions bedding (in the sense of Van Wagoner *et al.* 1990; Campbell, 1967) is actually present on a millimetre scale and is commonly produced by changes in detrital input associated with storm and tidal activity and then subsequently modified by bioturbation and diagenesis rather than by variations in anoxia/productivity. These observations have dramatic implications for high-resolution stratigraphic studies, because firstly, there is no reason why within a particular mudstone succession the sediments should record regional phenomena (for example an individual storm in one area is erosional, while elsewhere it is depositional). Secondly, given the very short time-period (days to weeks) of many of the

sedimentary processes operating on continental shelves relative to the time period recorded over a particular vertical interval, it is likely that most of the time represented in a mudstone succession is actually recorded on bedding planes rather than within beds (with hiatuses at this scale occurring in addition to those already recognized at shell-beds and concretionary horizons, e.g. Hudson & Martill 1994). Thirdly, the beds and bedding planes in mudstone successions which have been used as stratigraphical data for correlation purposes in the past, may not be recording short-lived bedding-related processes. Instead they may reflect much longer term sedimentary processes occurring at either a parasequence or parasequence-set scale, giving the correlations that are produced a significantly reduced resolution than commonly assumed.

Given these comments it is timely to investigate:

- the nature of 1 mm to 10 cm scale lithofacies variability within a mudstone succession that appears homogeneous at field scale;
- whether the small-scale facies, representing short time intervals can be traced laterally on 1 cm to 100 m scale;
- what are the dominant sediment transporting mechanism in the studied succession;
- what proportion of the sediment record is actually recorded in these mudstones and where, and on what scale, hiatuses are present.

Using data produced from such a study it should be possible to determine (a) the bed-scale variability within the studied mudstone succession, (b) whether or not this can be used reliably for correlation purposes and, if not, to determine at what scale (in terms of individual beds, bed-sets, or parasequences) realistic lateral correlations can be made, and (c) determine what sedimentary processes dominate the sedimentary record in the studied succession.

The Oxford Clay Formation

In order to investigate the aims mentioned above, the classic Oxford Clay Formation succession exposed at Saxon and King's Dyke Pits (national grid reference [TL248 965] and [TL248 967] respectively, Whittlesey, near Peterborough, working faces approximately 1.0 km apart) were investigated (see Hudson & Martill 1994 for location map). These were deemed particularly suitable as the rock exposed in these brickpits is not weathered. Moreover, the exceptional nature of the exposure means that reliable local correlation is possible for up to 1.0 km (see Fig. 1) and individual units can be easily related to published stratigraphies (e.g. Hudson & Martill 1994).

The mudstones of the Peterborough Member were deposited on a shallow marine shelf (e.g. Hudson & Martill 1991). At deposition the bottom waters were predominantly oxic as indicated by the scarcity of preserved lamination, the presence of bioturbation and an infauna dominantly comprising nuculaceans (Duff 1975). The preservation of lamination, and the presence of the biomarker isorenieretane (Kenig pers. comm. 1997) in some units (e.g. Bed 10 at Peterborough), however, suggests that the bottom waters were episodically anoxic.

The mudstones in this succession are predominantly composed of a range of dioctahedral micas (illite, illite/smectite and muscovite), quartz, calcium carbonate, siderite, pyrite and apatite (Norry *et al.* 1994). The carbonate comprises both autochthonous (e.g. coccoliths, foraminifera, bivalves and



Fig. 1. The Oxford Clay Formation succession exposed at Saxon Pit [SGR TL 248 965], Whittlesey, near Peterborough. Bed numbers after Hudson & Martill (1994). Face height is approximately 15 m.

ammonites) and diagenetic components. Analyses of successive mudstone units reveals that both upward-fining and upward-coarsening successions are present on a metre scale (e.g. Macquaker 1994). These upward-coarsening successions are capped by either cemented (calcite, dolomite) 'shell-beds', shell pavements or muddy sandstones. In contrast, the upward-fining successions are capped by either nodular carbonates or units unusually enriched in autochthonous components (e.g. foraminifera and coccoliths). The presence of upward-fining and upward-coarsening units suggests that during deposition of this succession the length of the sediment transport path varied perhaps in response to relative sea-level change. In addition, it is likely that the levels where the stacking patterns change (i.e. at 'shell-beds' and nodular carbonates) coincide with significant breaks in sediment accumulation. By analogy with similar mudstone successions elsewhere (e.g. Cleveland Ironstone Formation described by Macquaker & Taylor 1997; and the Kimmeridge Clay Formation Macquaker *et al.* in press) these levels are interpreted to be either close to, or mark, major stratal surfaces (e.g. maximum flooding surfaces). The upward-coarsening successions are combined highstand/forced regressive systems tracts and the upward-fining successions are transgressive systems tracts.

The basal units sampled as part of this study (Beds 14 to 17) have previously been described by Hudson & Martill (1994) as the 'most uniform part of the succession consisting of moderately organic-rich slightly fissile to blocky mudstones . . . which belong to the deposit-feeder shale biofacies of Duff (1975)'. The top part of the studied succession, Bed 18, is of the same biofacies and has been termed the 'dark bed' by Hudson & Martill (1994). The overall rates of sediment accumulation in the *Obductum* and *Grossouvrei* Subzones have been calculated by Hudson & Martill (1991) as being 10.7 mm ka^{-1} and 13.0 mm ka^{-1} respectively, with much of the time record probably accounted for during deposition of the dominant shell-beds (e.g. Bed 17).

Methods and nomenclature

In order to investigate the small-scale temporal lithofacies variability within the targeted part of the Peterborough Member, 48 samples were collected approximately every 0.15 m from the *obductum* to the

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grossouvrei Subzones, from Beds 14 to 18 (Fig. 1). This part of the succession was specifically targeted because it exhibited very little lithological change on a field-scale. Once the temporal lithofacies variability had been determined, lateral lithofacies changes were investigated by collecting 15 samples from three metres below the top of Bed 14 at 10 m intervals at different locations around Saxon Brick Pit, with three further sample locations from the same horizon in the neighbouring Kings Dyke Pit.

In order to determine the lithofacies present, a 20 µm thick polished thin section was made of each sample. These mudstones contain a significant water soluble component (mixed layer illite/smectite) consequently thin section preparation was performed utilizing paraffin as a cutting medium. The grain size, mineralogy and textures present were determined utilizing combined optical and electron optical techniques (backscattered electron imagery-BSE). Optical analyses were performed using a Nikon Optiphot Pol using Kodacolor 100 ASA gold and Ilford FP4 films, while electron optical analyses were performed using a JEOL 6400 electron microscope equipped with a Link 4-quadrant, solid-state backscattered electron detector. The microscope was operated at 20 kV, 2.0 nA, at an operating distance of 8 mm. Mineral identification was confirmed using a Link EDS detector attached to a Link EXL minicomputer operating in semi-quantitative mode. The grain size of the silt fraction was determined by measuring the long axis of 10 grains on the BSE photographs, while the absolute proportion of silt was semi-quantified using comparison charts (e.g. Flugel 1982) and is accurate to the nearest 5%. Further details of these techniques are given in Macquaker & Gawthorpe (1993).

In order to describe the lithofacies variability in the studied succession each mudstone sample was classified according to its grain size, mineralogy, grain origin and whether or not lamination was preserved using the terminology of Macquaker & Gawthorpe (1993), and Macquaker & Taylor (1996). This terminology is preferred to that of other users e.g. Potter *et al.* (1980) where all the mudstones studied here would be grouped into one category and simply termed 'claystones' making it impossible to distinguish subtle grain size trends between and within samples.

Results

The studied succession at Saxon Pit is illustrated in Fig. 1. The sampled locations and petrological details of each sample are presented in Table 1.

The sampled units comprise clay and silt-rich mudstones. These are predominantly composed of fine grained (<63 µm) mineral mixtures variously comprising illite, mixed layer illite/smectite, calcite, pyrite, and quartz with trace quantities of glauconite and kaolinite. The calcite is present as both shell fragments and cement. Selected samples are illustrated in Figs 2, 3 and 4.

Most samples are intensely bioturbated and exhibit compacted clay-filled, burrow mottling textures (sub-mm scale) produced by an unnamed meiofauna (Fig. 3a). In some samples, however, remnant upward-fining units (mm scale) are preserved (Fig. 3b). In these units sharp-based, more silt-rich laminae are overlain by clay-rich, silt-depleted laminae to form upward-fining couplets.

Detailed comparison of successive samples (Fig. 2) reveals that the mudstone lithofacies vary systematically throughout the studied succession in spite of their apparent homogeneity at hand specimen-scale. The individual samples were predominantly found to represent stacked metre-thick upward-coarsening units comprising clay-rich mudstones at their bases (silt:clay ratios <0.05) and silt-rich mudstones towards their tops (silt:clay ratios >0.05) (Figs 2 & 5). Each upward-coarsening succession is capped by either a shell-pavement or a shell-bed (in the sense of Kidwell *et al.* 1986). The units overlying the upward-coarsening successions are finer grained

clay-rich mudstones (compare Fig. 2a, b with Fig. 2c, d). These relationships are illustrated graphically (Fig. 5) with systematic variability in the changing silt:clay ratios.

Comparison of the shell-rich units at the top of each of the metre-scale upward coarsening units reveals systematic variations in faunal content (Fig. 5). Those from the basal 3.0 m are dominated by articulated, thin-shelled *Meleagrinella* sp. in contrast to those from the upper 2.0 m (including Beds 15 and 17) which are mainly disarticulated, thicker-shelled nuculaceans (e.g. *Mesosaccella* sp.). The major shell-beds (Beds 15 and 17) and the intervening unit (Bed 16) are particularly unusual as they are the coarsest intervals analysed in this study with silt:clay ratios of up to 0.22.

The lateral variability within samples collected from the same unit (3 m below the top of Bed 14) in Saxon and King's Dyke Pits (separated by 1 km) are shown (Table 1) and summarized in Fig. 5. These descriptions illustrate that these samples are surprisingly variable. For instance, while most of the samples collected from this unit are silt-rich mudstones, one (SP 14) is a clay-rich mudstone. In addition, the silt:clay ratios of these lateral samples vary significantly (0.03 to 0.12 see Table 1) and those from Saxon Pit are slightly finer grained than those from King's Dyke (compare Fig. 4a-f with Fig. 4g-l).

Discussion

The temporal lithofacies variability within this succession suggest that the sediment supply was variable. In the absence of any major changes in composition of the sediment the simplest way to interpret this variability is to assume that the length of the sediment transport path was varying through time rather than assuming that it was produced by sediment input variations. These changes could be caused by either delta lobe switching in the updip fluvial source region or by relative sea-level changes. The absence of lamination, horizons significantly enriched in nanoplankton and cemented units suggests that during deposition of this part of the Oxford Clay Formation (a) the bottom waters were never anoxic for extended periods, (b) productivity did not significantly vary, and (c) there were no prolonged breaks in sediment accumulation to allow pervasive cementation (e.g. Bottrell & Raiswell 1990; Macquaker & Gawthorpe 1993).

The apparent homogeneous nature of much of the succession makes it difficult to interpret the scale at which this variability is present (i.e. bed, bed-set, parasequence, etc.). In the absence of obvious field-scale lithological changes, the 1-5 m thick units have been previously termed beds for stratigraphic convenience (e.g. Callomon 1968; Duff 1975; Hudson & Martill 1994). Detailed analyses of these 'beds', however, reveals that they comprise a number of upward-coarsening units (up to 1 m thick) separated by shell-rich horizons and particularly fine-grained intervals. In sequence stratigraphic nomenclature upward-coarsening intervals separated by finer grained units are termed parasequences and marine flooding surfaces respectively (e.g. Van Wagoner *et al.* 1990). Given these detailed petrographic observations it seems more appropriate to describe these units as parasequence-sets rather than 'beds'.

Reinterpreting the 'beds' as parasequence-sets raises the question at what scale do beds (in the sense of Campbell 1967 and Van Wagoner *et al.* 1990) occur? From the earlier demonstration of metre-scale parasequence scale variability it follows

Table 1. *Semi-quantitative descriptions (%) of the Oxford Clay Formation mudstones sampled in Saxon and Kings Dyke Pits, Whittlesey, near Peterborough*

Sample no.	Depth (m)	Facies	Detrital silt	Detrital clay	Nanoplankton	Authigenic carbonate	Macro-shell debris	Pyrite	Authigenic clay	Visible organic matter
Saxon Pit	-3.15	Silt-rich mudstone	5.0	91.5	0.5	0.0	1.0	1.0	0.0	1.0
Saxon Pit	-3.0	Silt-rich mudstone	7.5	89.5	1.0	0.0	0.5	0.5	0.0	1.0
Saxon Pit	-2.85	Clay-rich mudstone	4.0	93.0	1.0	0.0	0.5	0.5	0.0	1.0
Saxon Pit	-2.7	Silt-rich mudstone	5.0	91.5	1.0	0.0	1.0	0.5	0.0	1.0
Saxon Pit	-2.55	Clay-rich mudstone	4.0	91.5	2.5	0.0	0.5	0.5	0.0	1.0
Saxon Pit	-2.4	Clay-rich mudstone	4.0	93.0	1.0	0.0	0.5	0.5	0.0	1.0
Saxon Pit	-2.25	Silt-rich mudstone	5.0	84.5	2.5	1.0	5.0	1.0	0.0	1.0
Saxon Pit	-2.1	Silt-rich mudstone	7.5	89.5	0.5	0.0	0.5	1.0	0.0	1.0
Saxon Pit	-1.95	Silt-rich mudstone	8.0	89.0	0.5	0.0	1.0	0.5	0.0	1.0
Saxon Pit	-1.8	Clay-rich mudstone	4.0	93.5	0.5	0.0	0.5	0.5	0.0	1.0
Saxon Pit	-1.65	Silt-rich mudstone	5.0	87.5	1.0	0.0	5.0	0.5	0.0	1.0
Saxon Pit	-1.5	Silt-rich mudstone	5.0	92.0	0.5	0.0	0.5	1.0	0.0	1.0
Saxon Pit	-1.35	Silt-rich mudstone	7.5	90.0	0.5	0.0	0.5	0.5	0.0	1.0
Saxon Pit	-1.1	Clay-rich mudstone	4.0	92.0	0.5	0.0	1.0	0.5	0.0	2.0
Saxon Pit	-1.05	Clay-rich mudstone	4.0	93.0	0.5	0.0	1.0	0.5	0.0	1.0
Saxon Pit	-0.9	Silt-rich mudstone	5.0	89.0	0.5	0.0	2.5	2.0	0.0	1.0
Saxon Pit	-0.75	Silt-rich mudstone	7.5	88.5	0.5	0.5	1.0	1.0	0.0	1.0
Saxon Pit	-0.6	Silt-rich mudstone	10.0	85.5	0.5	0.5	0.0	1.0	0.5	2.0
Saxon Pit	-0.45	Clay-rich mudstone	4.0	83.5	0.5	2.0	8.0	1.0	0.0	1.0
Saxon Pit	-0.3	Silt-rich mudstone	7.5	84.5	0.5	0.5	5.0	1.0	0.0	1.0
Saxon Pit	-0.15	Silt-rich mudstone	9.0	86.0	1.0	0.0	2.0	1.0	0.0	1.0
Saxon Pit	0.07	Silt-rich mudstone	15.0	68.0	0.5	5.0	10.0	0.5	0.0	1.0
Saxon Pit	0.21	Silt-rich mudstone	10.0	77.0	1.0	2.5	7.5	1.0	0.0	1.0
Saxon Pit	0.33	Silt-rich mudstone	12.5	70.0	0.5	0.5	15.0	0.5	0.0	1.0
Saxon Pit	0.53	Clay-rich mudstone	2.5	93.5	1.0	0.0	1.0	1.0	0.0	1.0
Saxon Pit	0.68	Silt-rich mudstone	6.0	91.5	0.5	0.0	0.5	0.5	0.0	1.0
Saxon Pit	0.83	Clay-rich mudstone	4.0	91.0	0.5	0.0	2.5	1.0	0.0	1.0
Saxon Pit	0.98	Clay-rich mudstone	4.0	93.5	0.5	0.0	0.0	1.0	0.0	1.0
Saxon Pit	1.13	Clay-rich mudstone	2.5	90.5	0.0	0.0	5.0	1.0	0.0	1.0
Saxon Pit	1.28	Silt-rich mudstone	5.0	92.5	0.5	0.0	0.0	1.0	0.0	1.0
Saxon Pit	1.43	Silt-rich mudstone	7.5	90.0	0.5	0.0	0.0	1.0	0.0	1.0
Saxon Pit 1	-3.0	Silt-rich mudstone	7.5	90.0	0.5	0.0	0.5	0.5	0.0	1.0
Saxon Pit 2	-3.0	Silt-rich mudstone	7.5	90.0	0.5	0.0	0.5	0.5	0.0	1.0
Saxon Pit 3	-3.0	Silt-rich mudstone	7.5	89.5	1.0	0.0	0.5	0.5	0.0	1.0
Saxon Pit 4	-3.0	Silt-rich mudstone	7.5	89.5	1.0	0.0	0.5	0.5	0.0	1.0
Saxon Pit 5	-3.0	Silt-rich mudstone	7.5	89.5	1.0	0.0	0.5	0.5	0.0	1.0
Saxon Pit 6	-3.0	Silt-rich mudstone	10.0	87.0	1.0	0.0	0.5	0.5	0.0	1.0
Saxon Pit 7	-3.0	Silt-rich mudstone	10.0	87.0	1.0	0.0	0.5	0.5	0.0	1.0
Saxon Pit 8	-3.0	Silt-rich mudstone	5.0	92.0	1.0	0.0	0.5	0.5	0.0	1.0
Saxon Pit 9	-3.0	Silt-rich mudstone	7.5	89.0	1.0	0.0	1.0	0.5	0.0	1.0
Saxon Pit 10	-3.0	Silt-rich mudstone	7.5	89.5	1.0	0.0	0.5	0.5	0.0	1.0
Saxon Pit 11	-3.0	Silt-rich mudstone	7.5	89.5	1.0	0.0	0.5	0.5	0.0	1.0
Saxon Pit 12	-3.0	Silt-rich mudstone	7.5	89.0	1.0	0.0	1.0	0.5	0.0	1.0
Saxon Pit 13	-3.0	Silt-rich mudstone	5.0	91.5	1.0	0.0	1.0	0.5	0.0	1.0
Saxon Pit 14	-3.0	Clay-rich mudstone	2.5	94.0	1.0	0.0	1.0	0.5	0.0	1.0
Saxon Pit 15	-3.0	Silt-rich mudstone	7.5	89.0	1.0	0.0	1.0	0.5	0.0	1.0
Kings Dyke 1	-3.0	Silt-rich mudstone	10.0	86.5	1.0	0.0	1.0	0.5	0.0	1.0
Kings Dyke 2	-3.0	Silt-rich mudstone	10.0	86.5	1.0	0.0	1.0	0.5	0.0	1.0
Kings Dyke 3	-3.0	Silt-rich mudstone	10.0	86.5	1.0	0.0	1.0	0.5	0.0	1.0

The sample depths are given relative to the top of Bed 14 of Hudson & Martill (1994)

that the bedding thicknesses are likely to be significantly less than 1 m once again, however, field observations do not provide any obvious bedding structures at this scale. Detailed petrographic observations show that thin (millimetre-thick), upward-fining units are present in some samples and that bioturbation has commonly disrupted many of these structures. By analogy with similar sedimentary structures described elsewhere (e.g. Pedersen 1985) these thin upward-fining couplets are interpreted to be the depositional products of waning flow systems in distal locations on the sediment transport path (see also Macquaker & Taylor 1997) and

probably produced by storms. Moreover, as these are discrete events separated by periods of non-deposition (as indicated by the presence of an infauna, see below) and produce units which show internal laminae the millimetre-thick couplets are interpreted to be beds in a genetic sense.

Where remnant bedding is still visible; the presence of burrowing meiofauna, and the absence of an aerobic trace fossil assemblage suggests that below the sediment/water interface porewater conditions were dysaerobic rather than fully aerobic and there was insufficient time between storm events for the sediment to be fully colonized. In contrast where the

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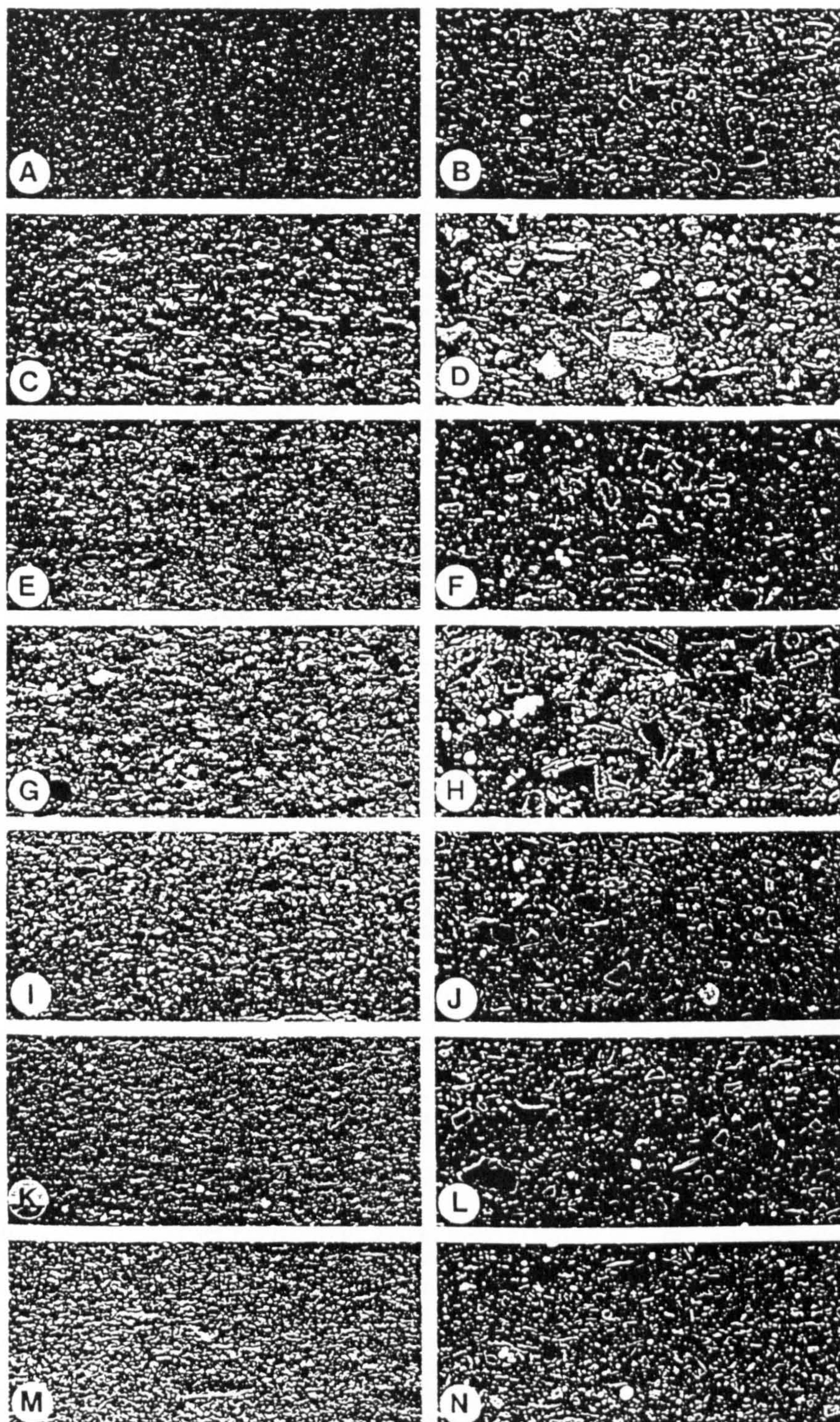


Fig. 2. Backscattered electron and optical photomicrograph pairs illustrating the vertical facies variability in the mudstones of Peterborough Formation in Saxon Pit. The samples were collected from the top of Bed 14, Bed 15, Bed 16, Bed 17 and the base of Bed 18 of Hudson & Martill (1994). (a, b) Sample SP 0.53 m, clay-rich mudstone from close to the base of Bed 18, silt:clay ratio: 0.03. (c, d) Sample SP 0.33 m, silt-rich mudstone collected from within a shell bed (Bed 17), silt:clay ratio 0.18. (e, f) Sample SP 0.21 m, silt-rich mudstone collected from within Bed 16, silt:clay ratio 0.13. (g, h) Sample SP 0.07 m, silt-rich mudstone collected from basal part of shell bed (Bed 15). Note the presence of abundant broken shell fragments and relatively coarse detrital quartz grains, silt:clay ratio 0.22. (i, j) Sample SP -0.15 m, silt-rich mudstone collected from the top of Bed 14, silt:clay ratio 0.10. (k, l) Sample SP -0.30 m, silt-rich mudstone collected from within Bed 14, silt:clay ratio 0.13. (m, n) Sample SP -0.45 m, clay-rich mudstone collected from within Bed 14 just above a shell pavement, silt:clay ratio 0.05. Field of view of optical micrographs 0.27 mm. Field of view of BSEI micrographs 270 μ m.

original bedding has been destroyed it seems most probable that the sediment had been completely bioturbated between storm events and that the pore waters were predominantly oxic. The presence of this variability suggests that where couplets are visible then net sediment accumulation rates were relatively more rapid than in units where the original sedimentary structures have been destroyed.

The preceding discussion leads on to the stratigraphic status of the shell beds and shell pavements within this succession. Our analyses demonstrate that these units are intimately

associated with the flooding surfaces between parasequences rather than between bedding planes. In general, shell beds form where there is reduced clastic dilution of the bioclastic components (e.g. Kidwell 1988, 1989). Given the stratigraphic constraints imposed by their distribution, it is envisaged that these shell-enriched units formed either prior to maximum marine flooding in environments where there was dynamic bypass; or just post-marine flooding in environments associated with a period of increased accommodation availability. In practical terms, however, distinguishing between these two

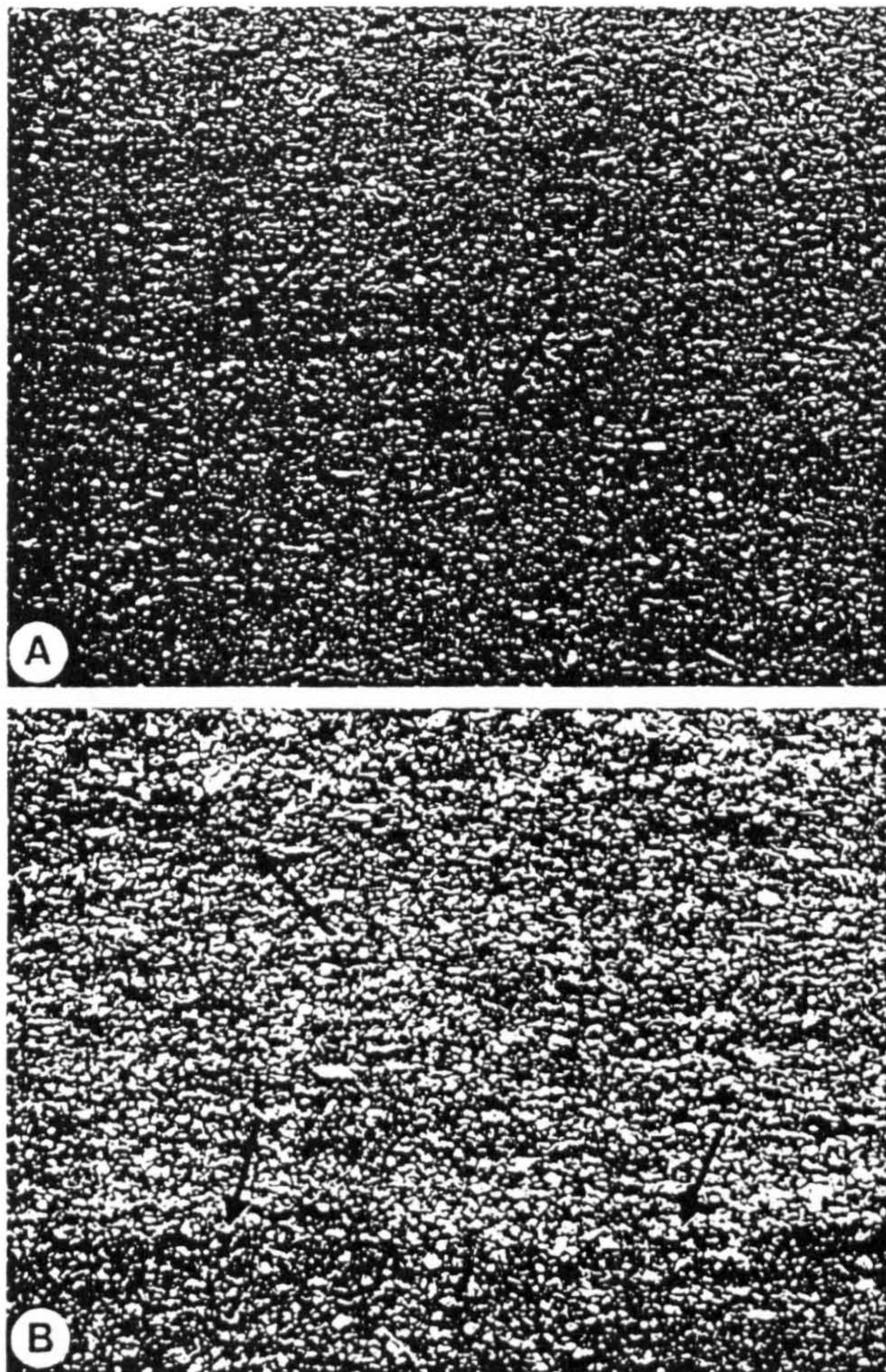


Fig. 3. (a) Optical micrograph of silt-rich mudstone from sample depth - 30 m illustrating the flattened clay-filled burrows (arrowed). The ichnogenera are an unnamed meiofauna. Field of view 0.4 mm. (b) Optical micrograph of a silt-rich mudstone from sample depth 0.07 m illustrating the mm-scale remnant upward-fining that is present within some samples. Note the presence of a sharp-based silt-rich lamina (arrowed L) which is overlain by a finer-grained clay-rich lamina (arrowed C) which together form an upward-fining couplet. Field of view 0.4 mm.

distinct stratigraphic settings is difficult as they occur at similar locations at the top of upward-coarsening successions. It is interesting to note, however, that comparison of the various shell-enriched units shows that there are some systematic faunal and grain size differences. For instance, the shell pavements in the bottom 3 m of the succession, are dominated by relatively thin shelled *Meleagrinella* sp., while thicker shelled nuculaceans are found in the upper 2 m of the succession. Moreover, the shell-beds in the upper part of the succession have the highest silt:clay ratios of any units studied. While these characteristics are not absolutely diagnostic, they do suggest that the processes which caused shell-enrichment within the Oxford Clay Formation may have varied stratigraphically and they also hint at larger-scale stacking variability (i.e. at a systems tract-scale) being present in this succession. Our dataset at this larger-scale is however, limited and this discussion is not developed further here.

The lateral variability of samples collected on a 10 m scale suggests that bed-scale (in a genetic sense) correlation, even

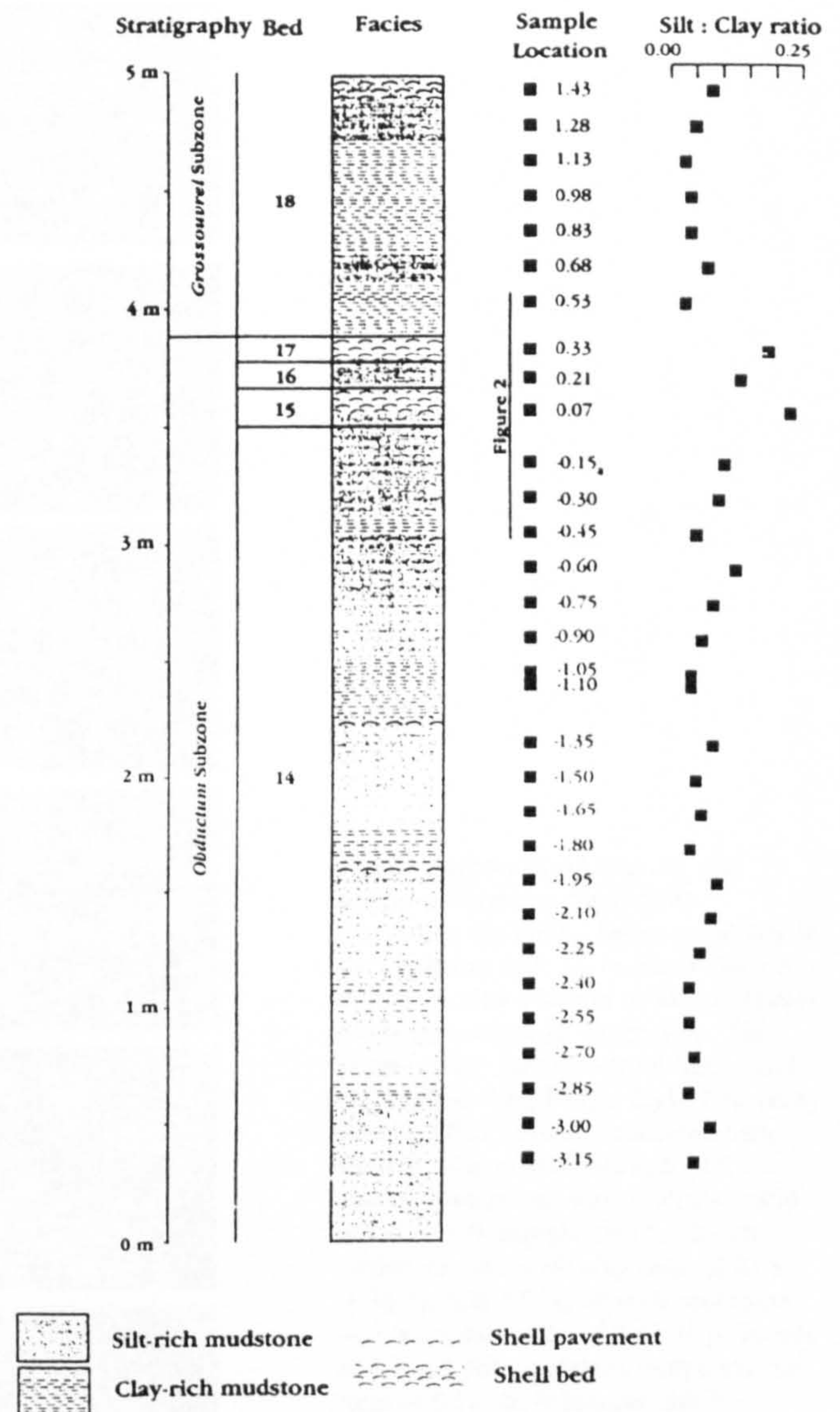


Fig. 4. Sedimentological log illustrating the facies variability within the Oxford Clay Formation between Beds 14 and 18 (Bed numbers after Hudson & Martill 1994) exposed in the succession at Saxon Pit, Whittlesey, near Peterborough, UK.

over short distances is very difficult. At a simplistic level, it is possible to argue that this demonstrates there is lateral facies variability on a 10 m scale. This view has to be tempered with the facts that (a) that individual beds (in a genetic sense) are very thin, (b) adjacent beds can be rather different and (c) much of the original bedding has been homogenized by bioturbation. Given that the beds are so thin and that we neither collected samples with the necessary resolution (on a millimetre scale) nor were the thin sections prepared from precisely located horizons we believe that slight vertical sampling errors are probably responsible for the observed lateral facies variability. Given these comments additional, extremely detailed, work will be required to determine just how far individual beds can be traced laterally and how variable the facies are over these intervals. Our data, however, do suggest that bed-scale correlation, for practical purposes, is virtually impossible in this succession.

Reinterpreting the scale of the stacking patterns in this succession, with bedding planes on a millimetre-scale,

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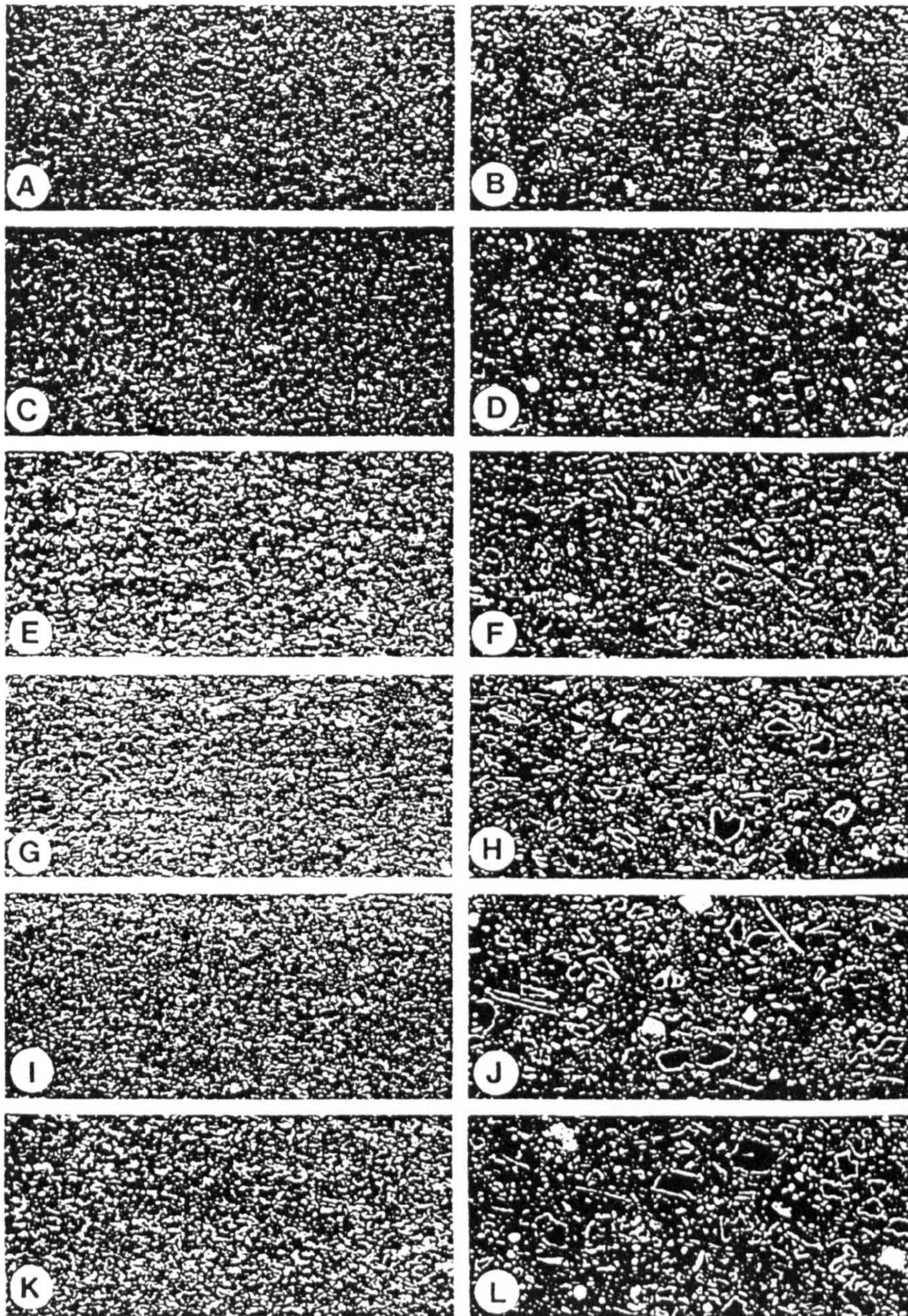


Fig. 5. Backscattered electron and optical photomicrograph pairs illustrating the lateral facies variability in the mudstone unit 3.0 m below the top of Bed 14 after Hudson & Martill (1994) of the Peterborough Formation. The samples were collected from Saxon and the neighbouring King's Dyke Pits. (a, b) Sample SP13, silt-rich mudstone with a silt:clay ratio of 0.05. (c, d) SP 14, clay-rich mudstone with a silt:clay ratio of 0.03. (e, f) Sample SP 15, silt-rich mudstone with a silt:clay ratio of 0.08. (g, h) Sample KD 1, silt-rich mudstone with a silt:clay ratio of 0.12. (i, j) Sample KD 2, silt-rich mudstone with a silt:clay ratio of 0.12. (k, l) Sample KD 3, silt-rich mudstone with a silt:clay ratio of 0.12. Field of view of optical micrographs 0.27 mm. Field of view of BSEI micrographs 270 μ m.

parasequences on a metre-scale and stacked parasequence on a 5 m scale makes it simpler to explain why the overall rates of sediment accumulation are so slow. Previously researchers (e.g. Hudson & Martill 1991, 1994) have argued that there were significant diastems at the major shell beds with cryptic diastems elsewhere. This study suggests that the newly recognized parasequence boundaries and bedding planes are excellent candidates for these diastems.

Conclusions

Combined optical, electron optical microscopy and sedimentary logging reveals that the lithofacies in the studied succession include clay-rich mudstones, silt-rich mudstones 'shell pavements' and 'shell beds'. Most of the mudstones studied were intensely bioturbated but some exhibited remnant upward-fining couplets at a millimetre scale. Laminated mud-

stones, concretionary carbonates and nanoplankton-rich mudstones, which have been observed elsewhere in the Oxford Clay Formation and other siliciclastic mudstone successions, were not encountered.

In this succession six upward-coarsening intervals (metre-scale) were observed. The upward-coarsening successions are composed of clay-rich mudstones at their bases and silt-rich mudstones at their tops. 'Shell pavements' were found in the lower 3 m of the succession between the upward-coarsening successions. In contrast 'shell beds' were found in the upper 2 m of the succession between the upward-coarsening intervals.

Samples collected from closely spaced locations laterally indicate that there is significant lithofacies variability. These data, however, are difficult to interpret as the individual beds are very thin, and much of the succession has been partially homogenized by bioturbation. Consequently it is not possible to determine unequivocally if 'true' bed-scale lateral facies variations are present. These data, however, do suggest that

for all practical purposes lateral correlation at a bed-scale in this type of succession is impossible, and that high resolution correlations using these data in this type of succession can only be made at a bed-set or greater-scale.

The presence of systematic, temporal lithofacies variability within this succession suggests there were significant variations in the relative length of the sediment transport path through time, either produced by delta-lobe switching updip in the fluvial source or, by relative sea-level change. There was no evidence in this part of the succession that systematic changes in either surface productivity or bottom water anoxia significantly influenced the lithofacies produced.

The bioturbated, millimetre-scale upward-fining couplets are interpreted to be beds with upward-fining being consequent upon storm deposition. The colonization of the sediment between storm events by a meiofauna has obscured most of the internal structures of these units and is interpreted to indicate that there were significant time intervals between storms. In the light of this observation it is probable that the millimetre-scale hiatuses (i.e. bedding planes) represent much of the time record. Hiatuses are thus not only occurring at the major shell-beds and concretionary horizons, but also on flooding surfaces between parasequences and on bedding planes.

The metre-scale, stacked upward-coarsening successions are interpreted to be parasequences. The levels between the parasequences, where there is rapid sediment fining, are interpreted to be marine flooding surfaces. The parasequences are interpreted to have been produced by shoaling following rapid deepening. The varying styles of shell-enrichment (shell pavements developed at the top of the basal three parasequences and shell beds at the upper three parasequences) coupled with systematic large scale variations in grain size suggest that sequence scale variations may be present. In the absence of lateral data on a regional scale it is not possible, however, to assign the shell-beds to specific stratal surfaces.

Finally, the presence of so much vertical variability within this apparently homogenous mudstone succession, coupled with the fact that there is lateral grain size variability on a 0.1 to 1.0 km scale indicates that making unequivocal, high-resolution (bed-scale) correlations at a basin-scale within units like the Oxford Clay Formation are likely to be fraught with uncertainty.

We are grateful to the following people for constructive criticism of earlier drafts of this manuscript: H. Shaw, P. Wignall, D. Pirrie, C. Curtis and J. Hudson. In addition, we would like to thank the other researchers in the Oxford Clay Working Group for making otherwise very boring rocks very interesting! Finally J.W. would like to thank the Open University and her supervisors (D. Martill and P. Sheldon) for support and encouragement throughout her PhD.

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APPENDIX FIVE

Figure A5.1 illustrates both the 'a' and 'b' values for the Length to Height ratio for *M. morrisi*, Calvert Pit.

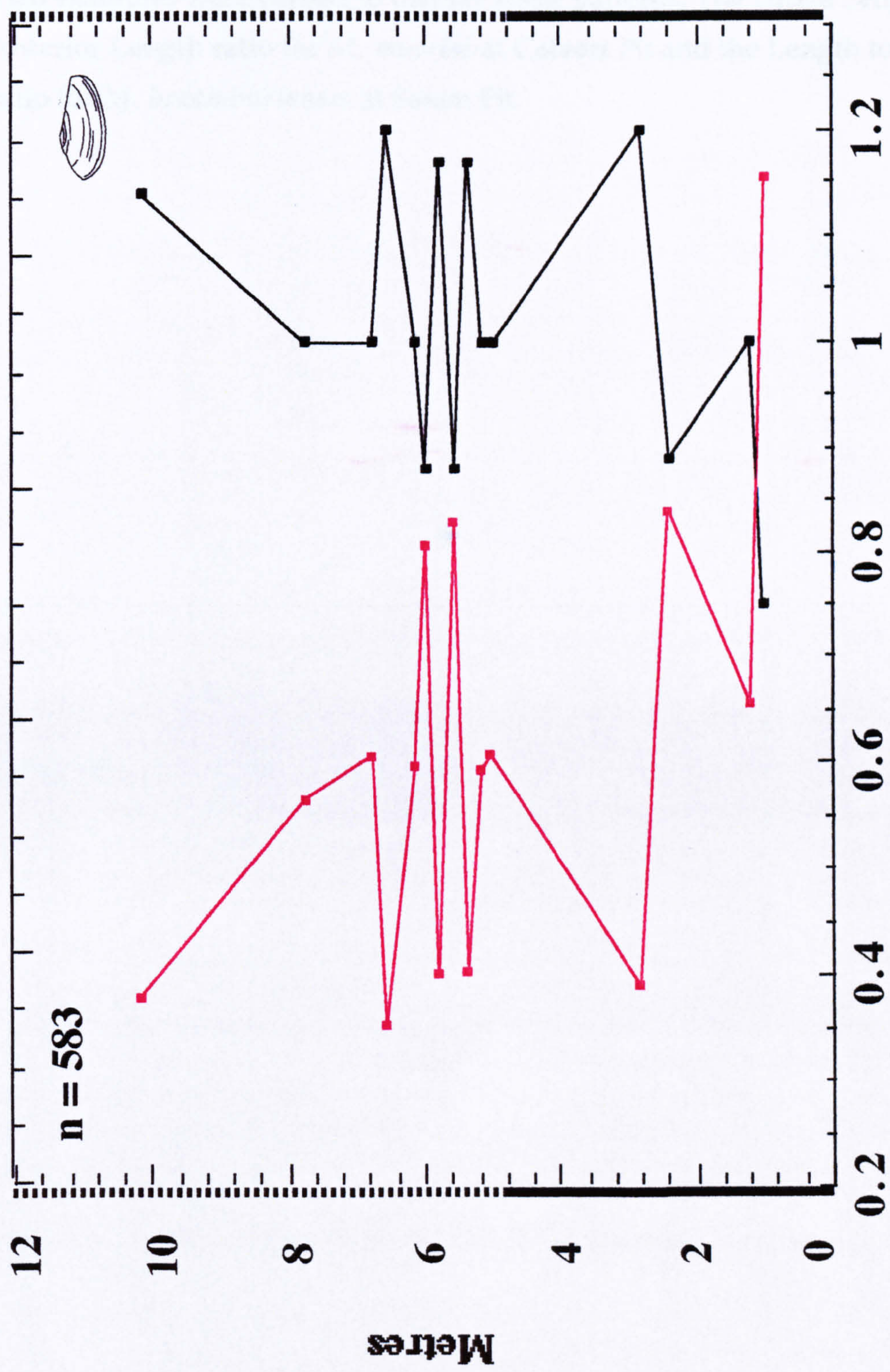


Figure A5.1. 'a' and 'b' values for the Length to Height ratio for *Mesosaccella morrisi*, Calvert pit.
Black Squares are 'a' values; Red Squares are 'b' values (For data see Table A2.4).

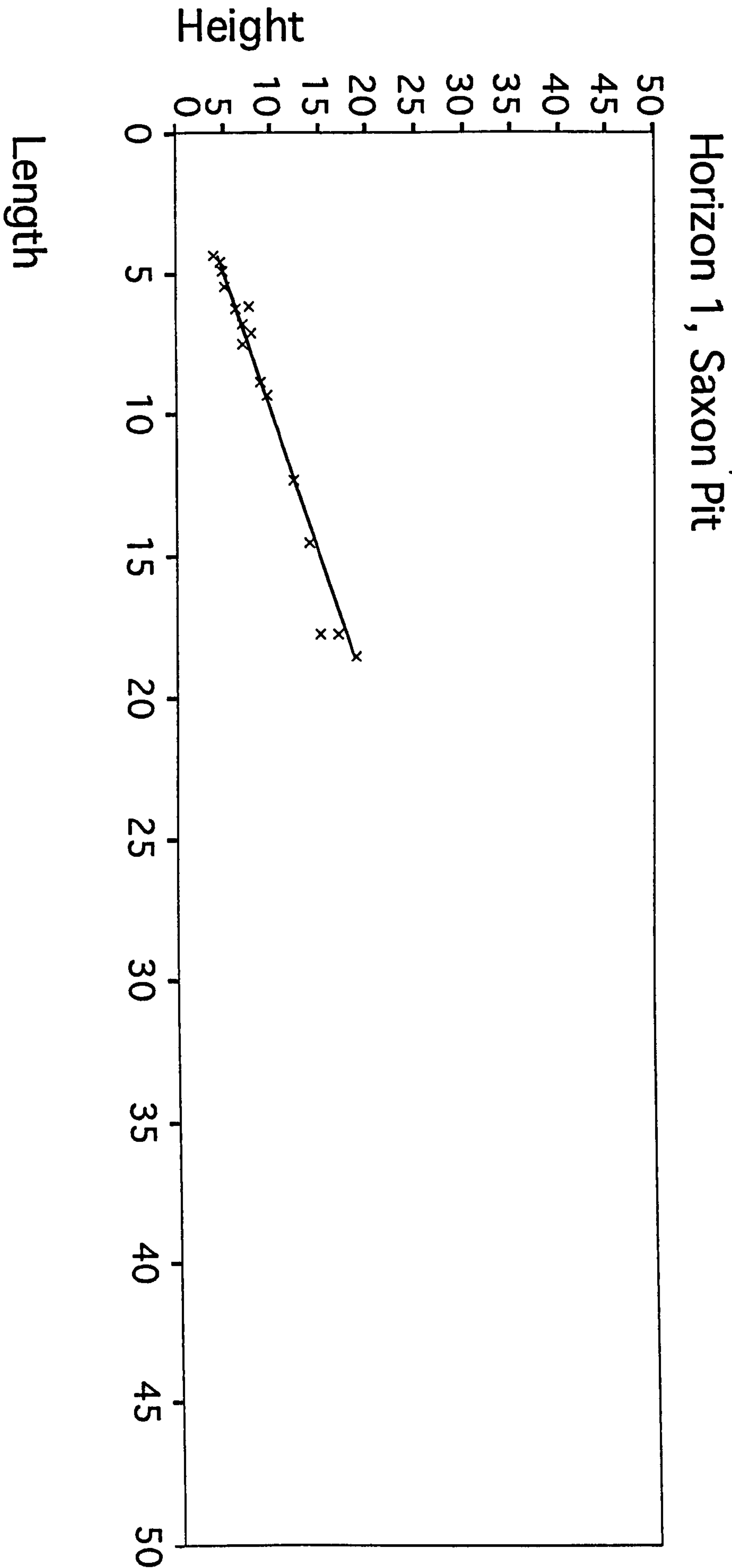
APPENDIX SIX

Some examples of individual patterns of relative growth with individual data points.

Two examples were chosen to display these patterns, The Hinge Length to Anterior Length ratio for *M. morrisi* at Calvert Pit and the Length to Height ratio for *M. braamburiensis* at Saxon Pit.

Pattern of Relative Growth

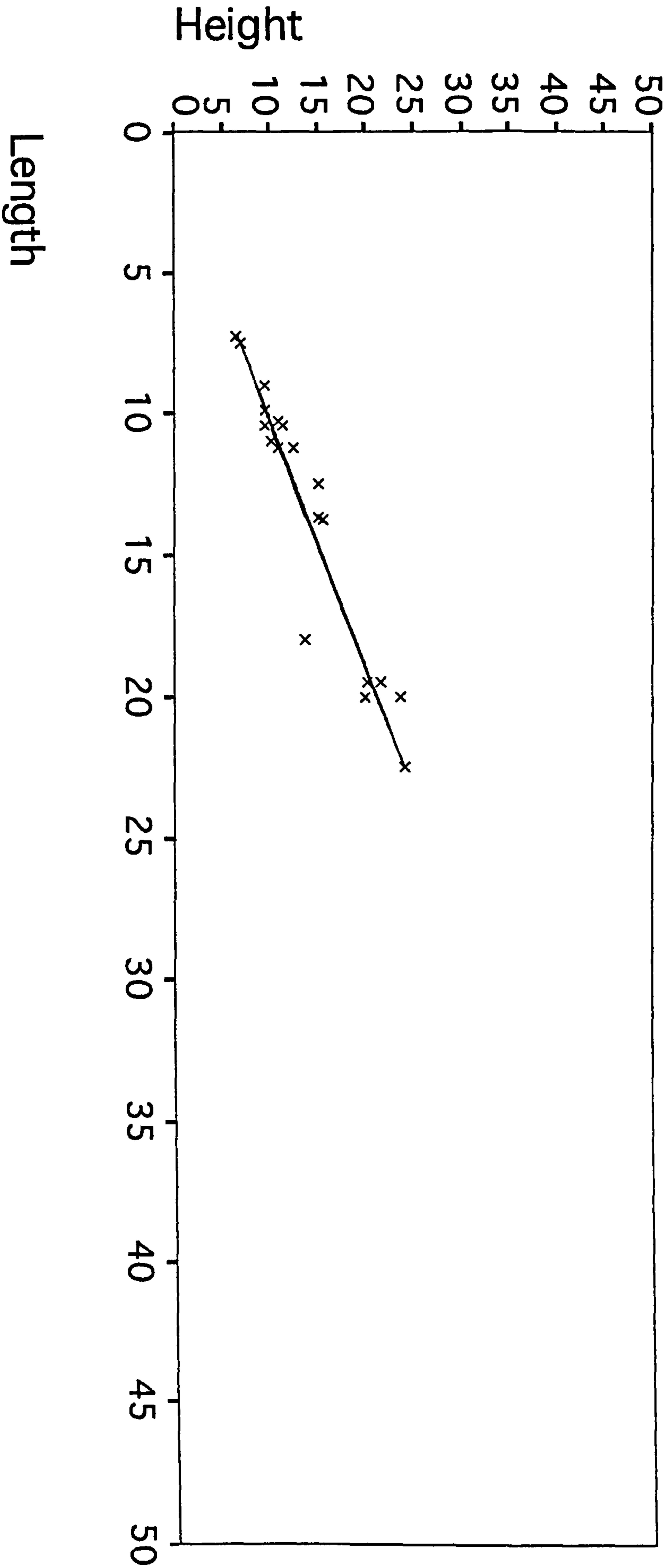
Height against Length, for *M. braamburiensis*



Pattern of Relative Growth

Height against Length, for *M. braamburiensis*

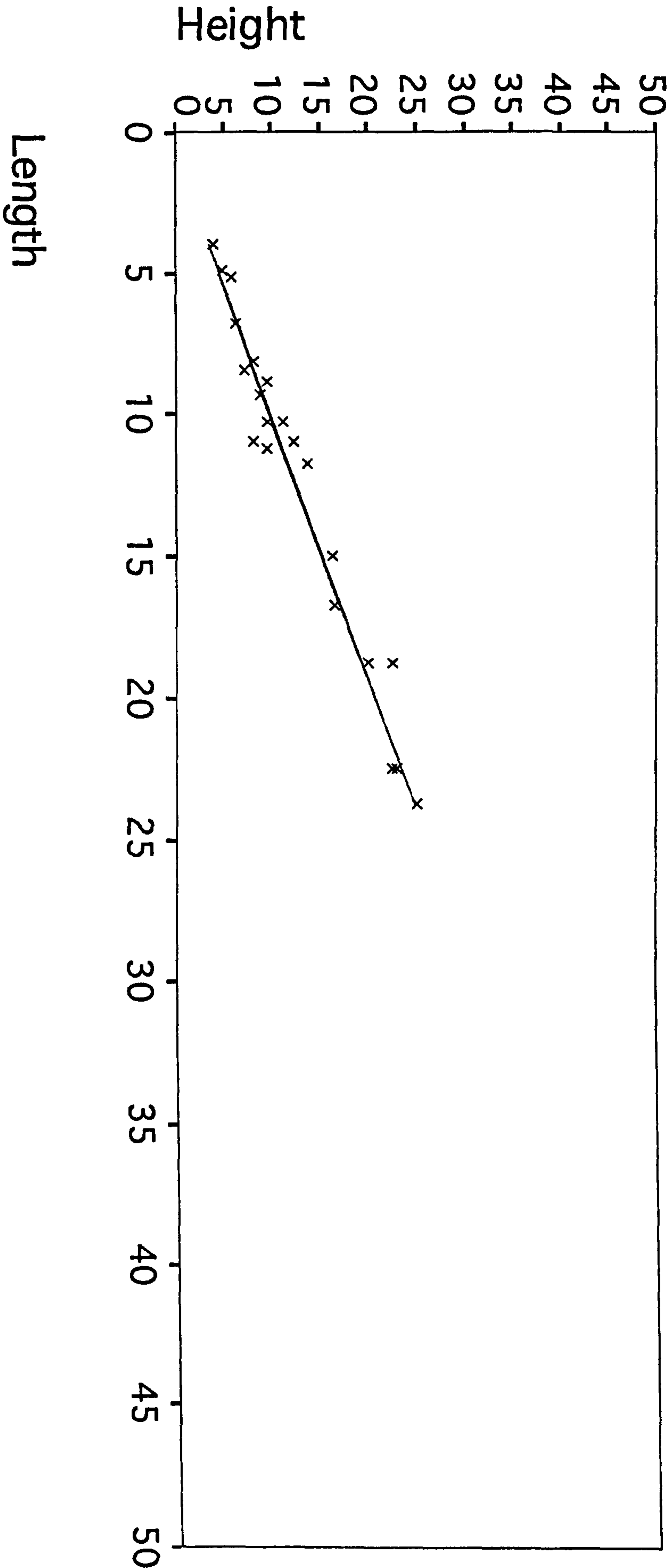
Horizon 3, Saxon Pit



Pattern of Relative Growth

Height against Length for *M. braamburiensis*

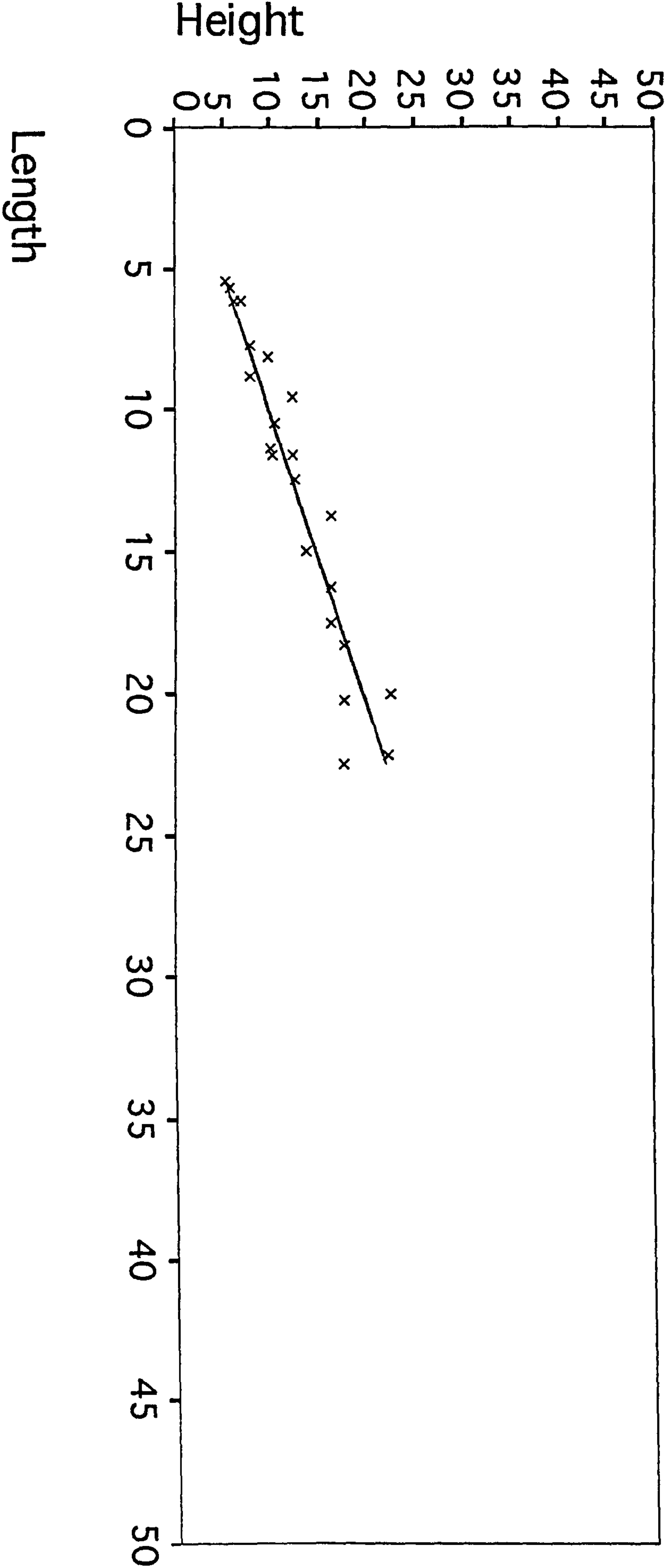
Horizon 6, Saxon Pit



Pattern of Relative Growth

Height against Length, for *M. braamburiensis*

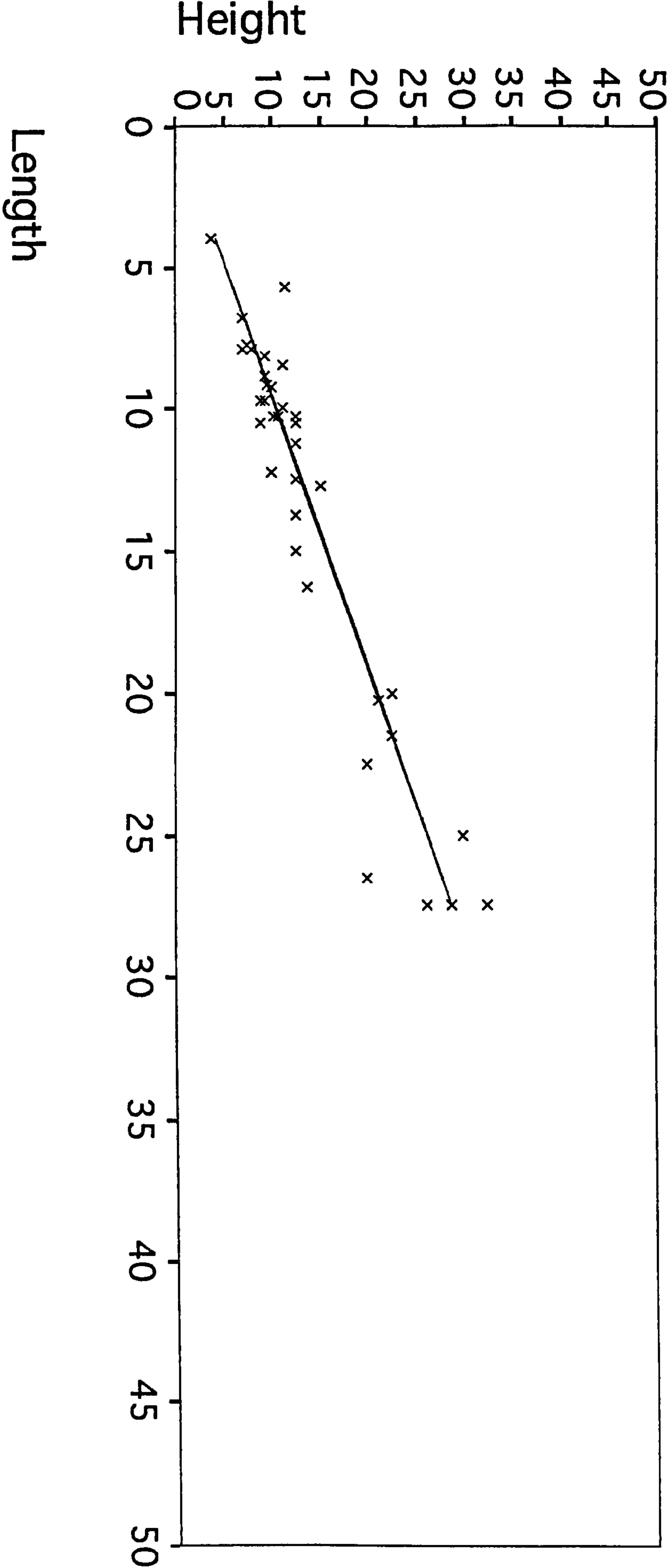
Horizon 9, Saxon Pit



Pattern of Relative Growth

Height against Length

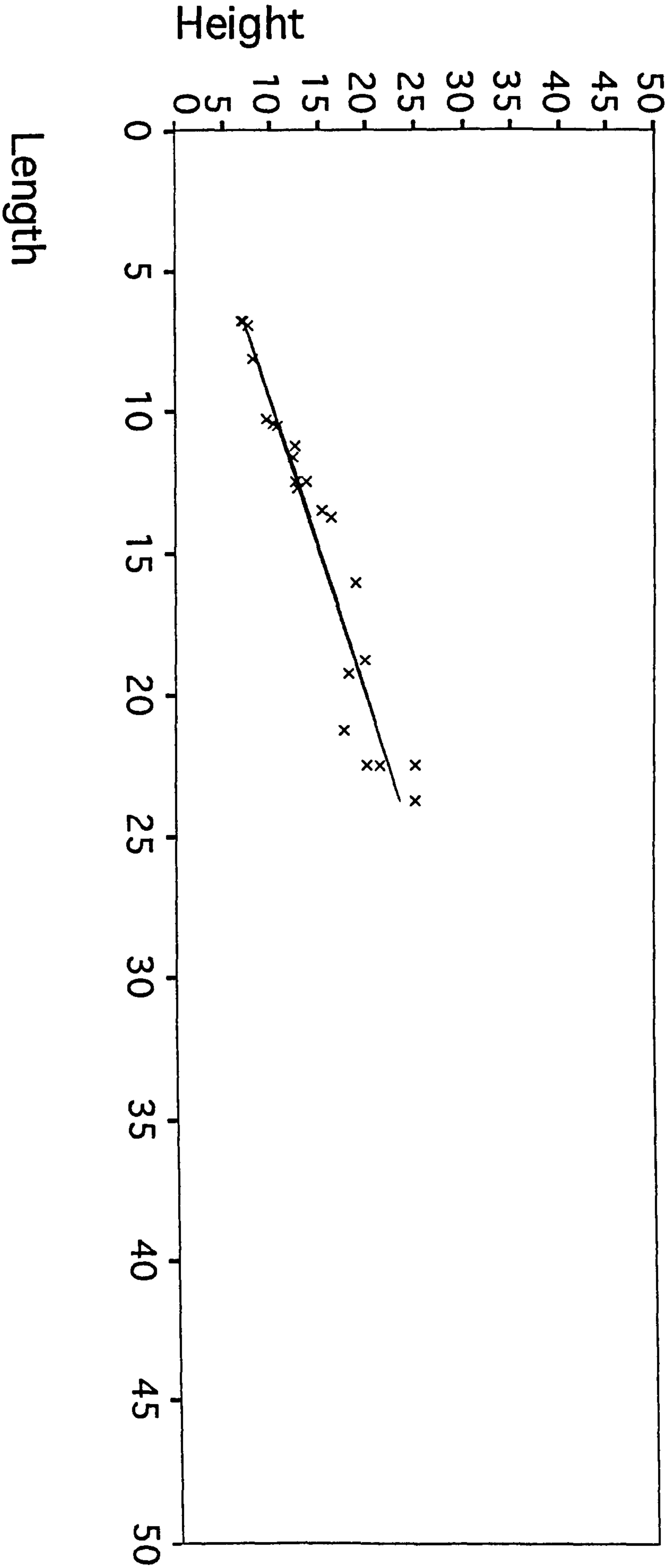
Horizon 13, Saxon Pit



Pattern of Relative Growth

Height against Length, for *M braamburiensis*

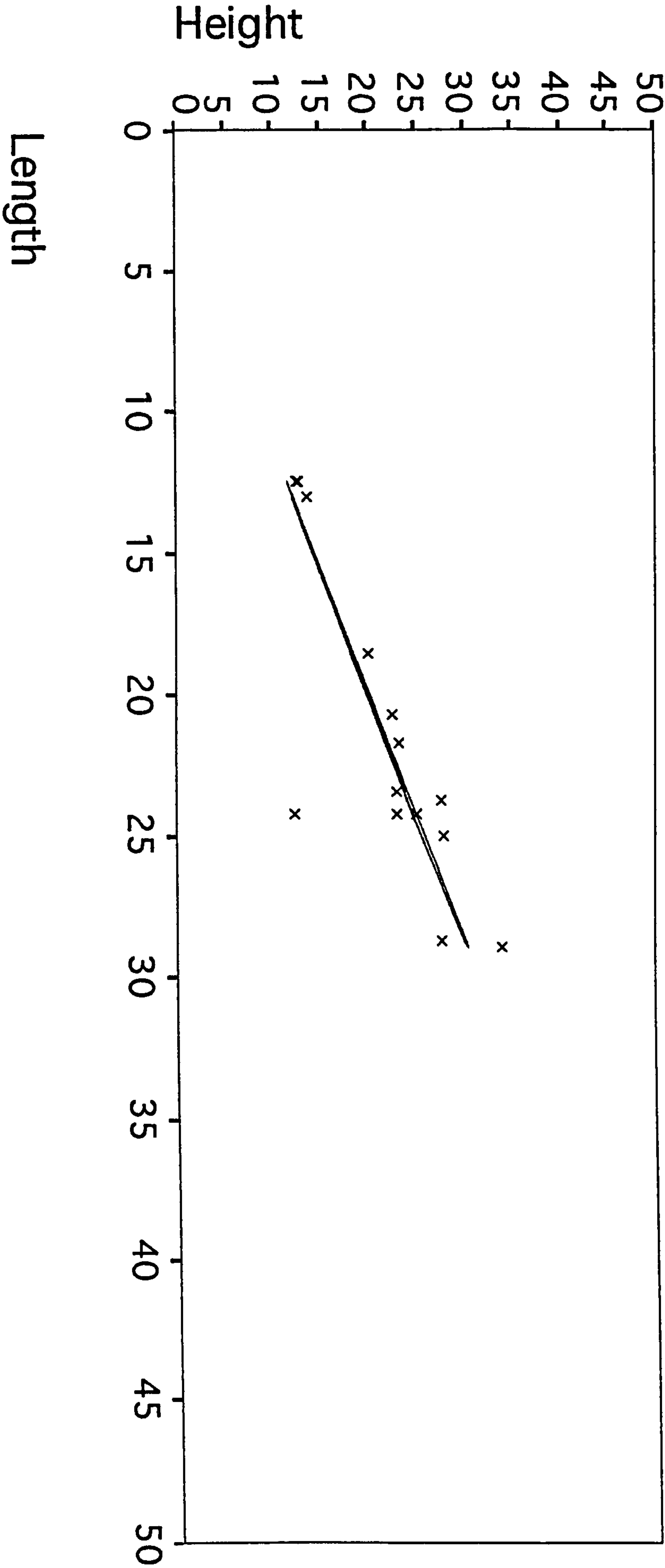
Horizon 15, Saxon Pit



Pattern of Relative Growth

Height against Length, for *M. braamburiensis*

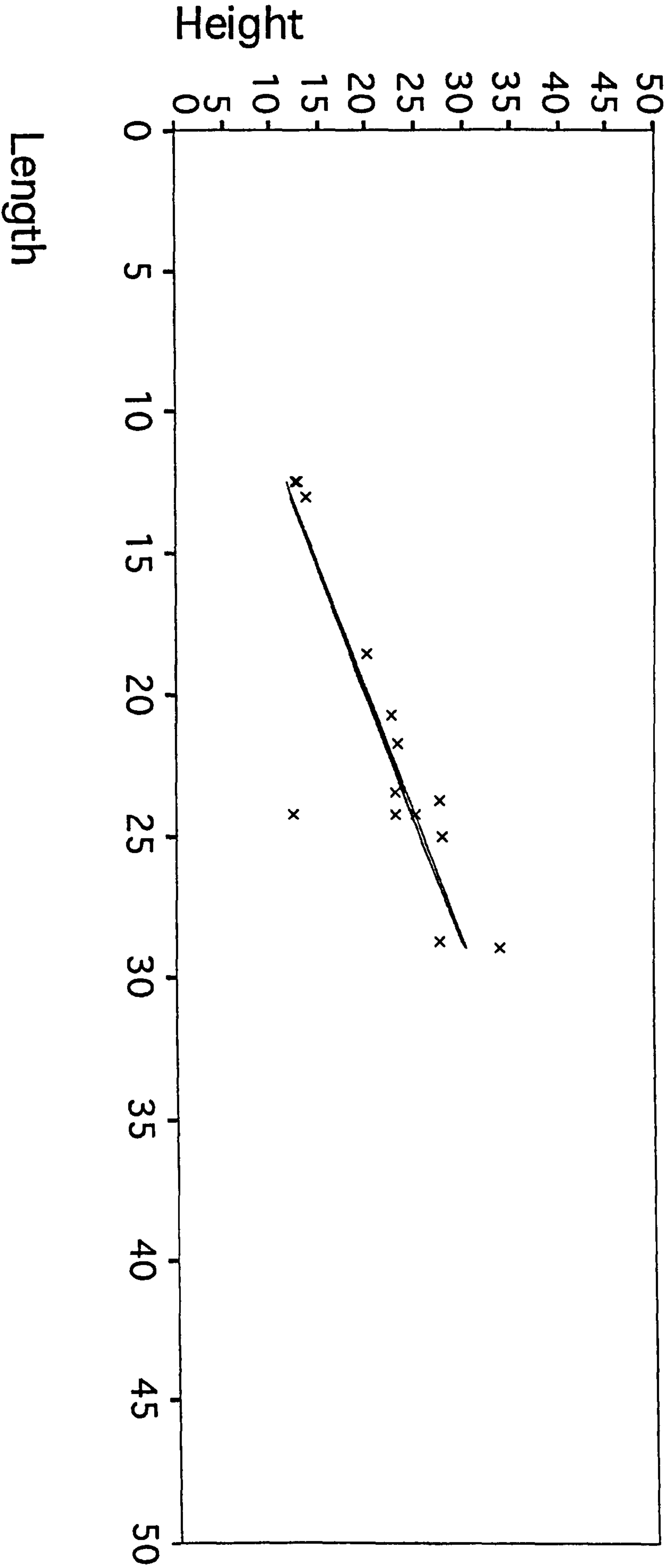
Horizon 28, Saxon Pit



Pattern of Relative Growth

Height against Length, for *M. braamburiensis*

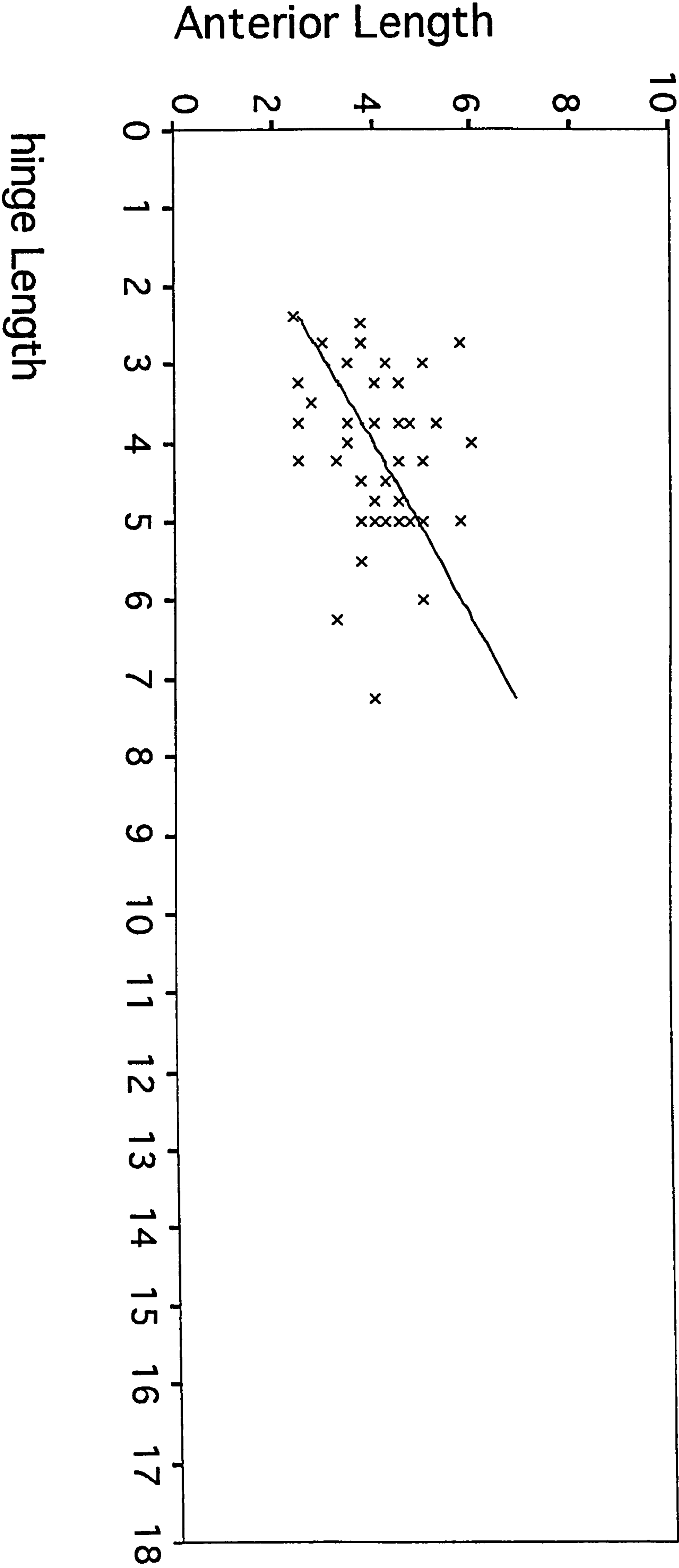
Horizon 28, Saxon Pit



Pattern of Relative Growth.

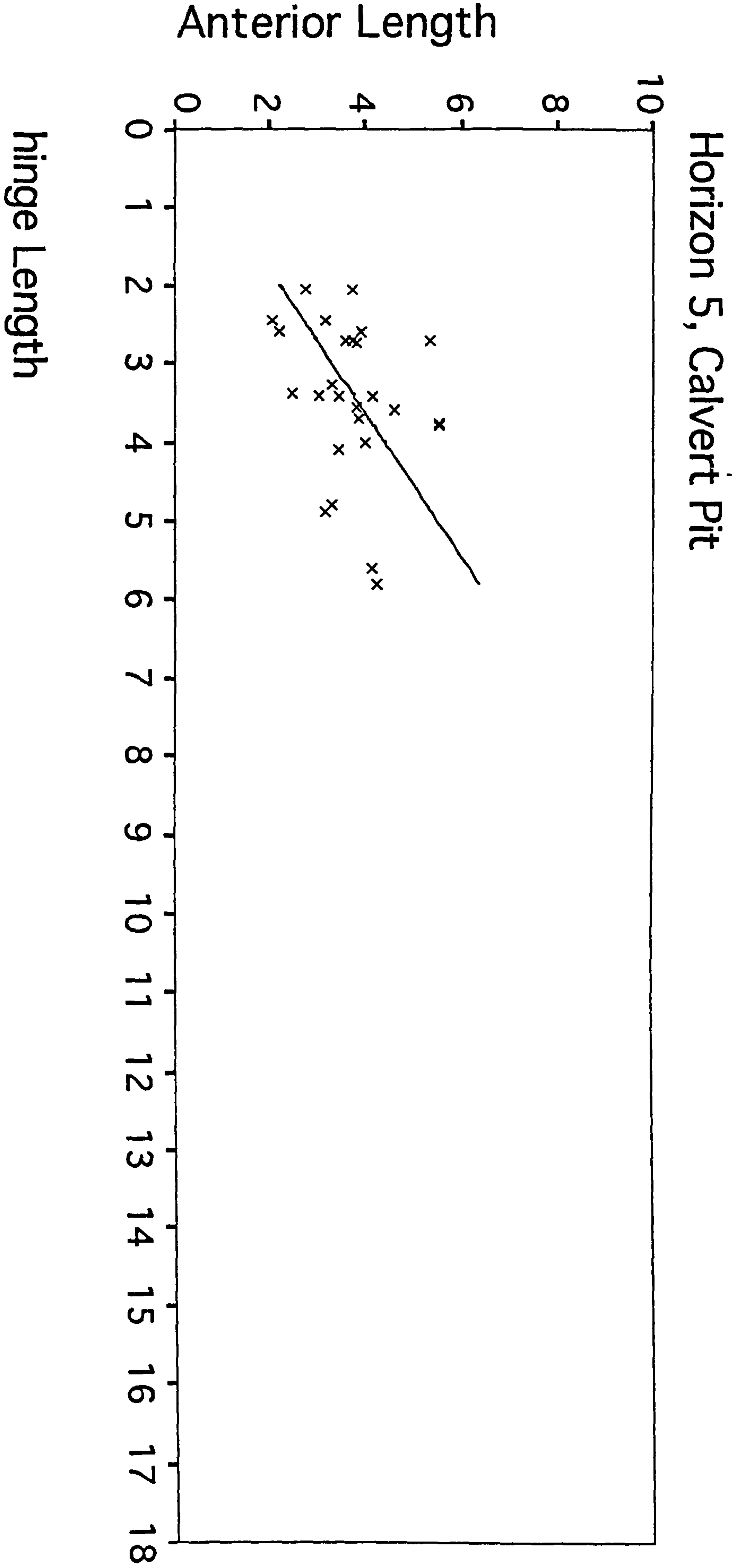
Anterior Length against hinge Length, for M. Morrisi

Horizon 4, Calvert Pit



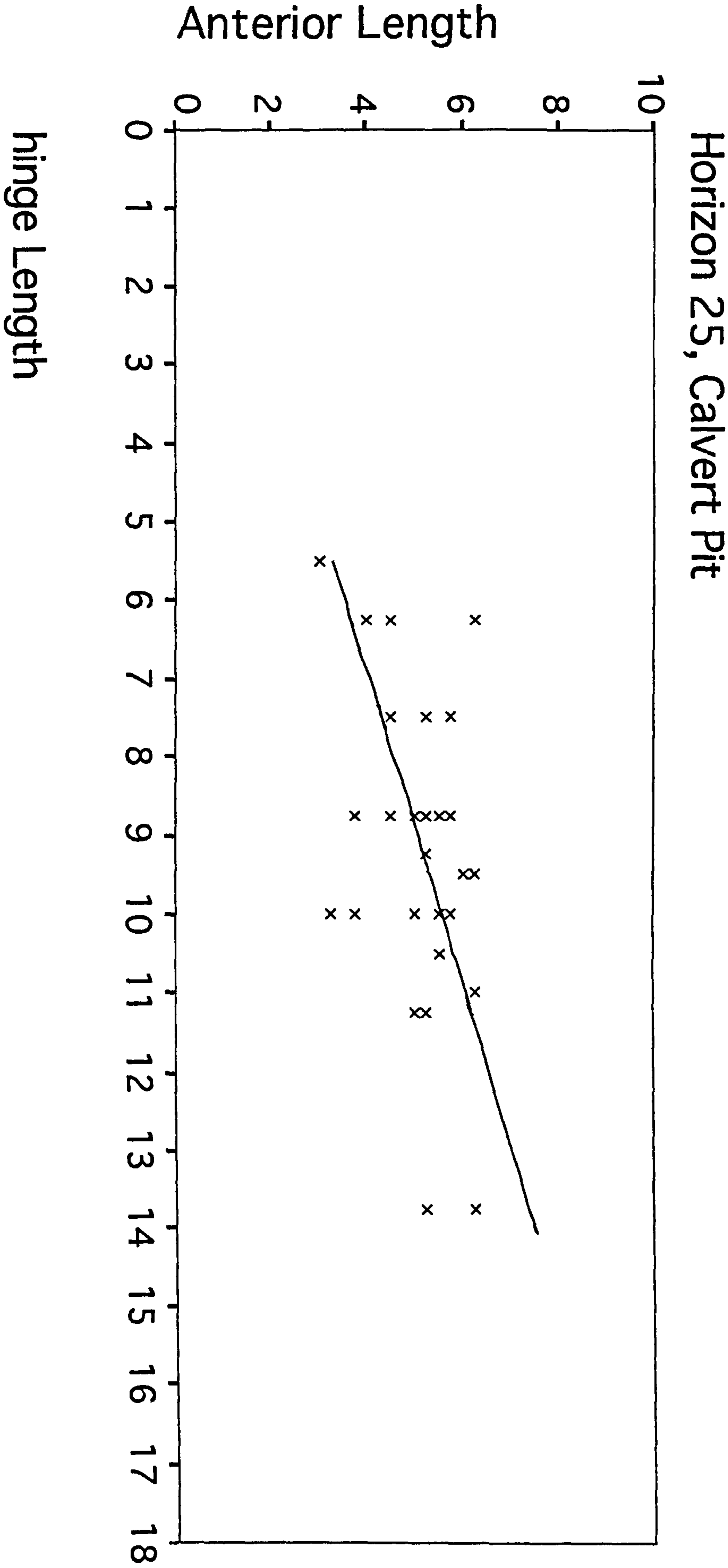
Pattern of Relative Growth

Anterior Length against hinge Length, for *M. morrisi*



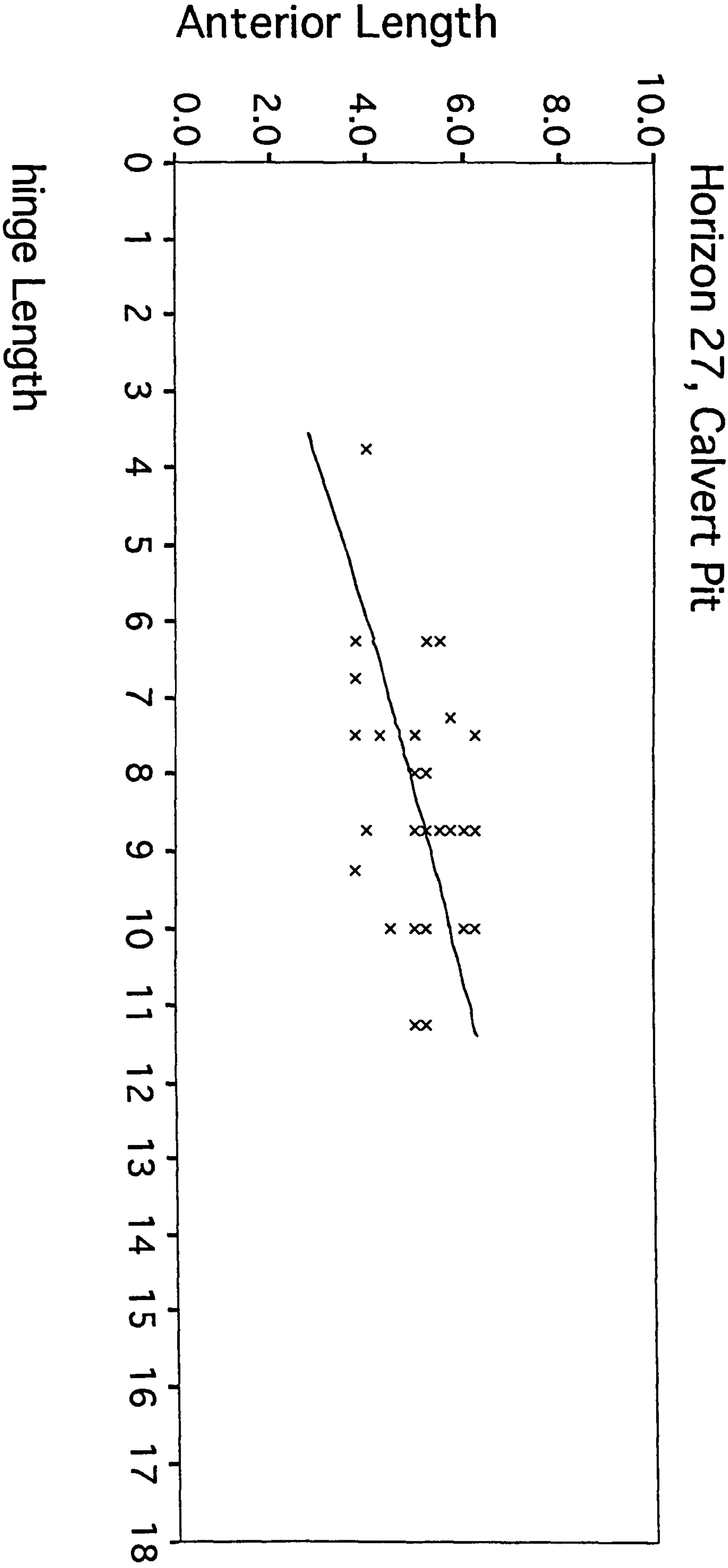
Pattern of Relative Growth

Anterior Length against hinge Length, for *M. morrisi*



Pattern of Relative Growth

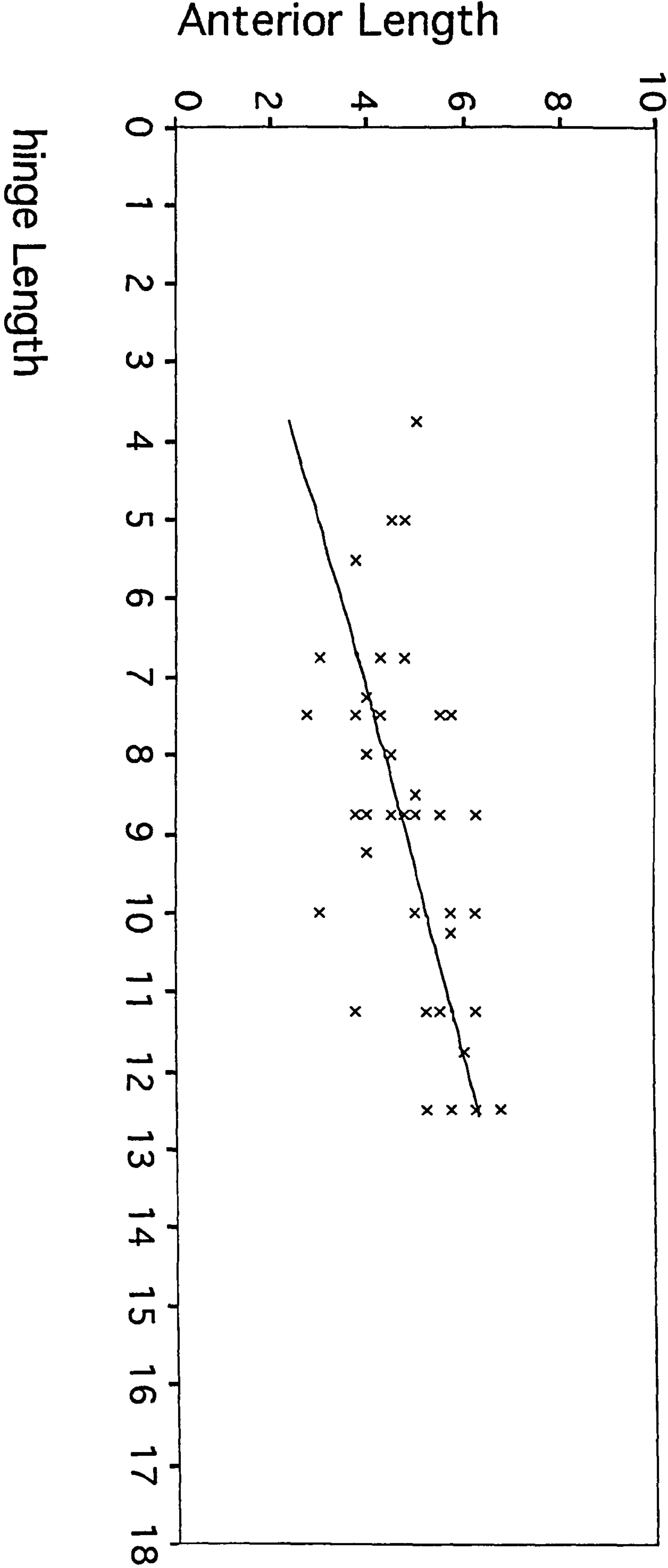
Anterior Length against hinge Length, for *M. Morrisi*



Pattern of Relative Growth

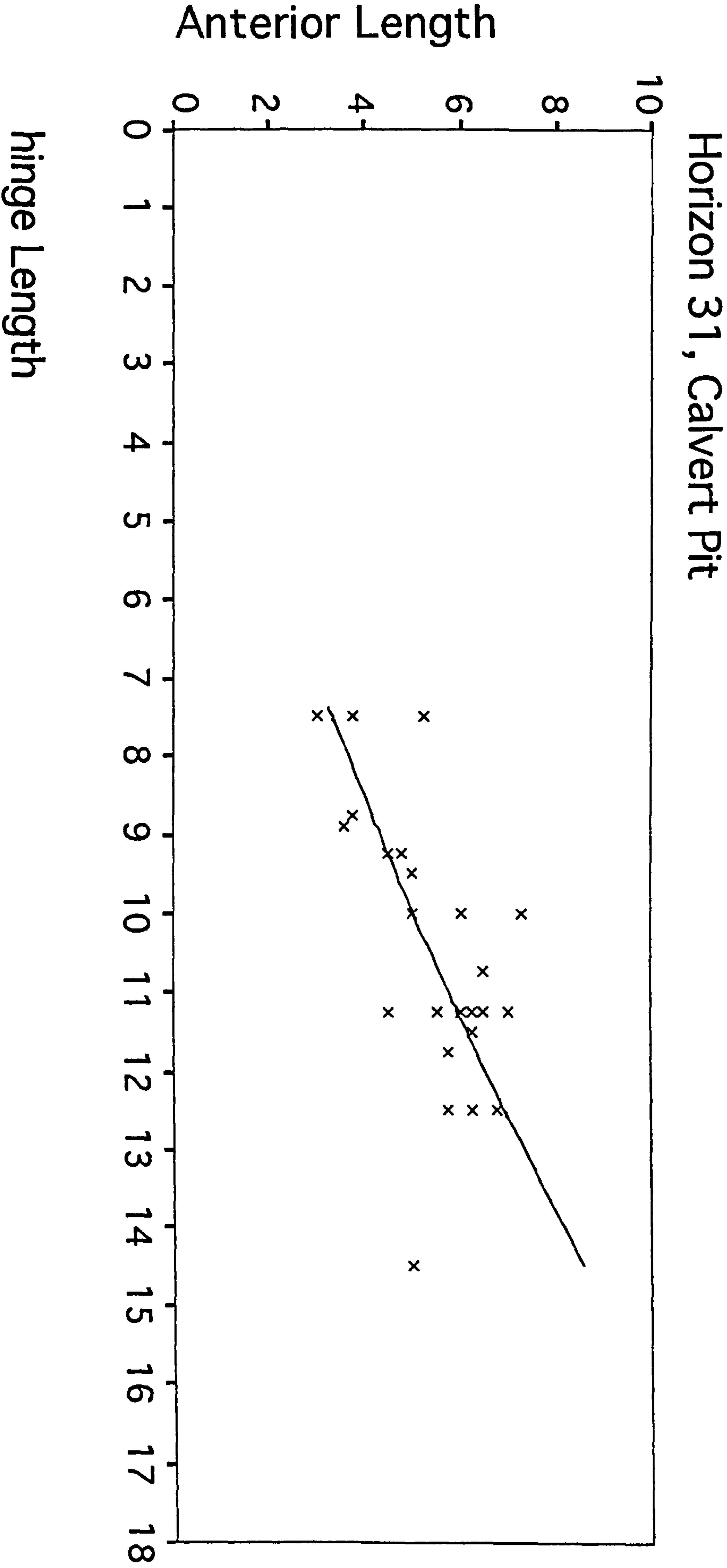
Anterior Length against hinge Length, for *M. morrisi*

Horizon 29, Calvert Pit



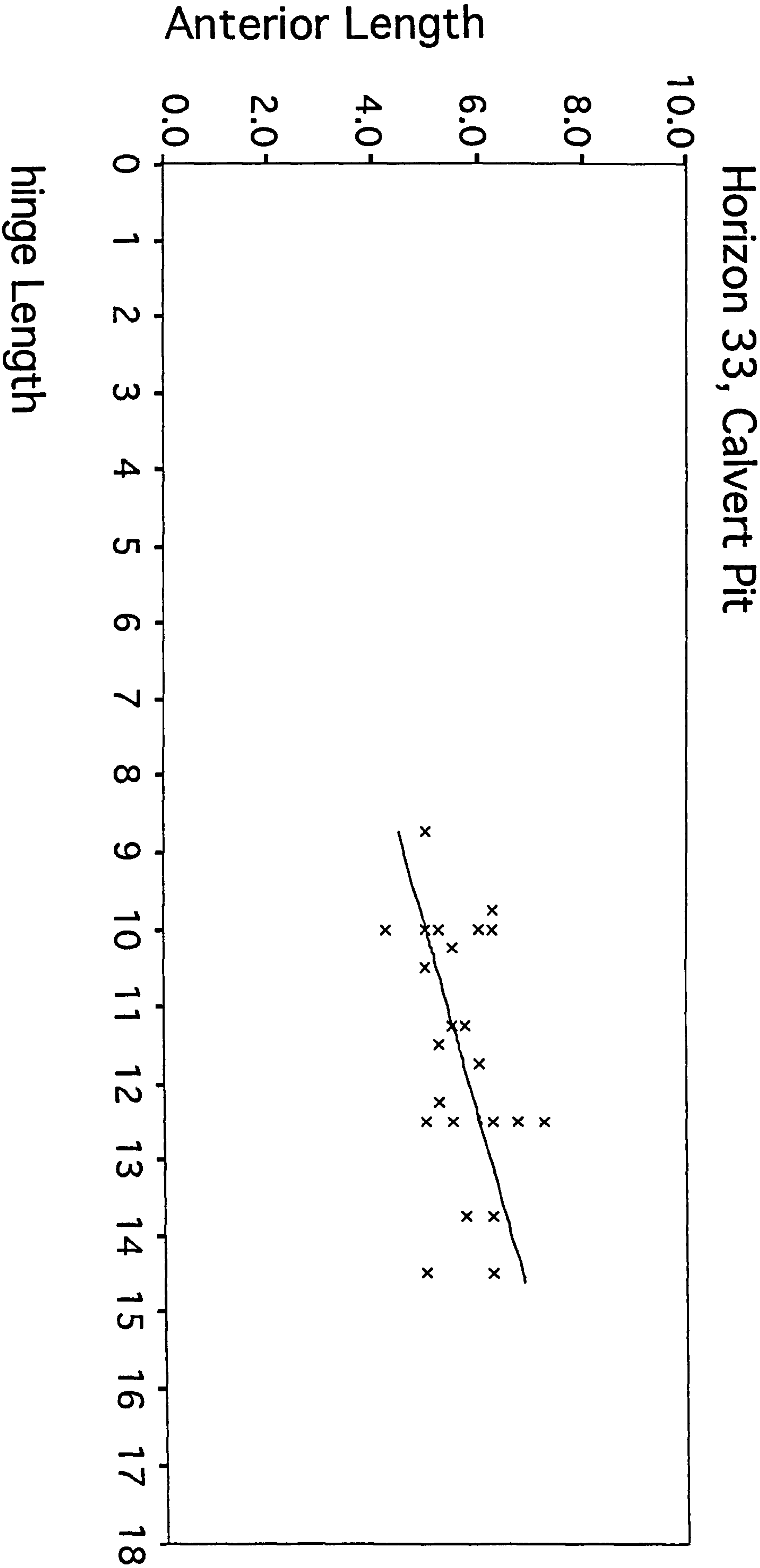
Pattern of Relative Growth

Anterior Length to hinge Length, for *M. morrisi*



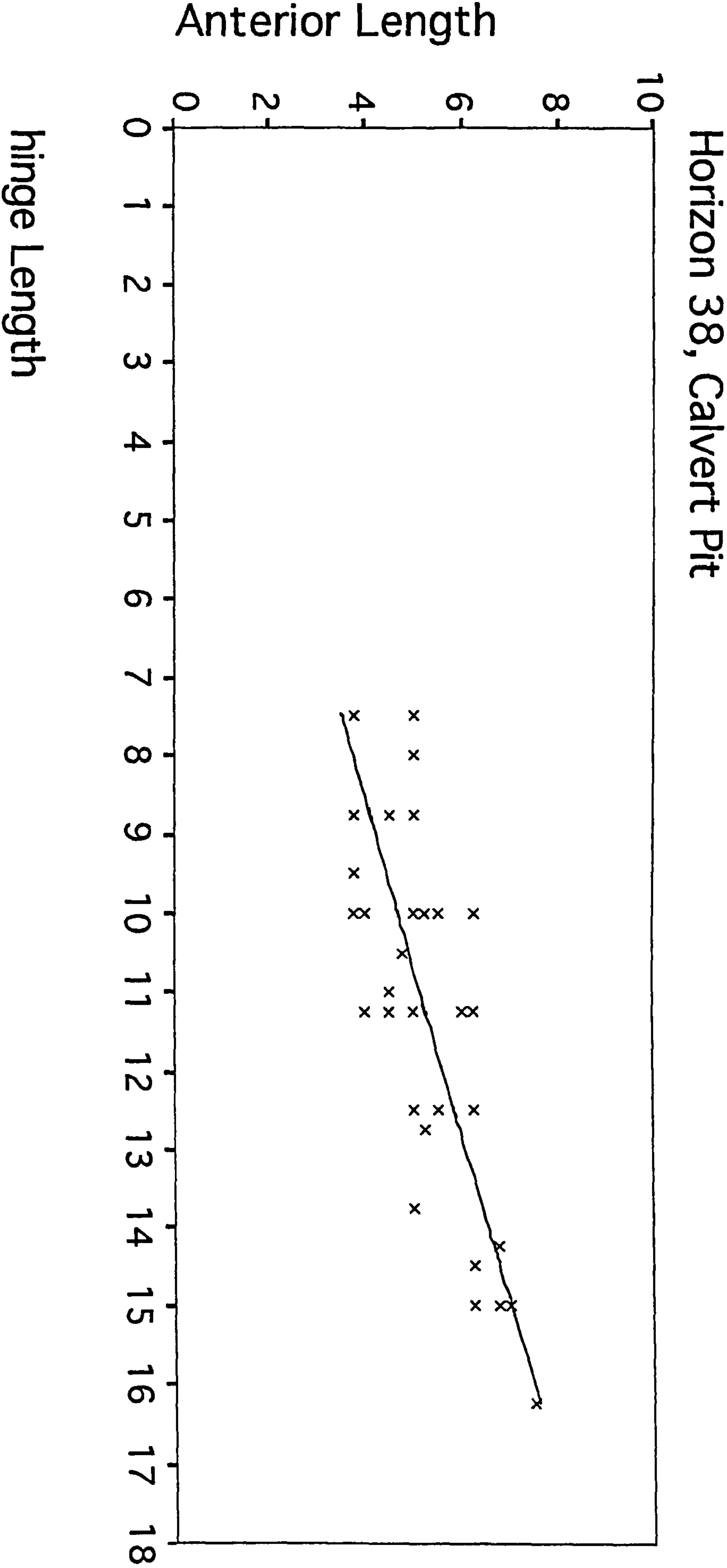
Pattern of Relative Growth

Anterior Length against hinge Length, for *M. morrisi*



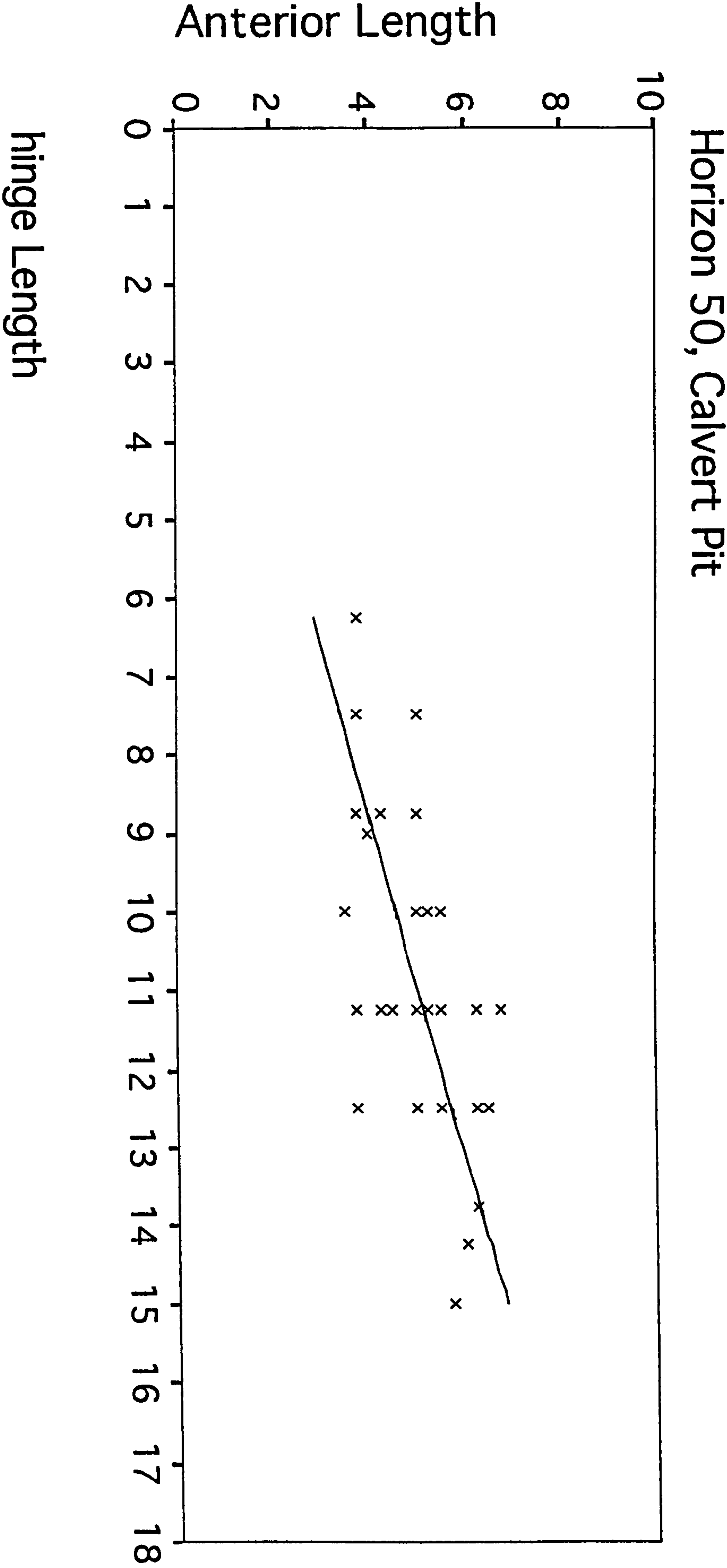
Pattern of Relative Growth

Anterior Length against hinge Length, for *M. morrisi*



Pattern of Relative Growth

Anterior Length against hinge Length, for *M. morisi*



APPENDIX SEVEN

A copy of the complete set of original data used to graph the results seen in Chapter 7, has been placed in the Open University Library, Milton Keynes. If anyone should require the original data a copy can be gained from:.

The Library

The Open University

Walton Hall

Milton Keynes

MK7 6AA

The original specimens are also housed within the Open University. Anyone wishing to study these may contact:

The Department of Earth Sciences

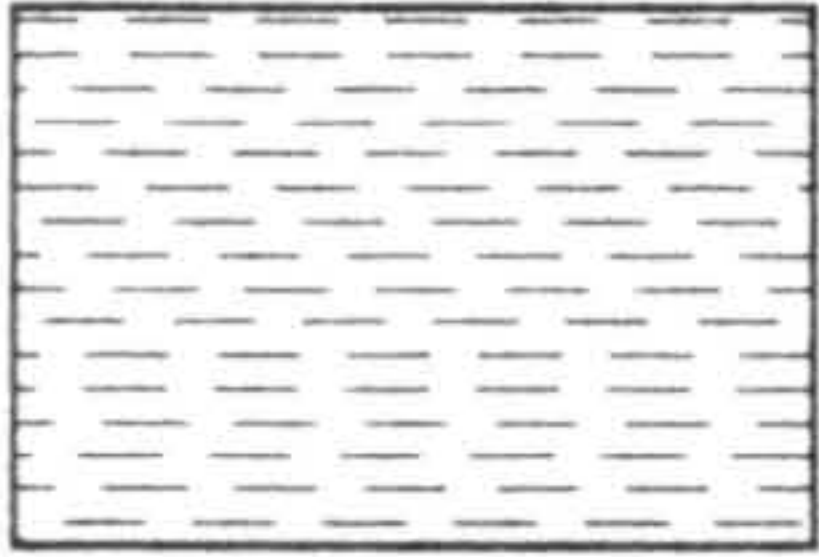
The Open University

Walton Hall

Milton Keynes

MK7 6AA

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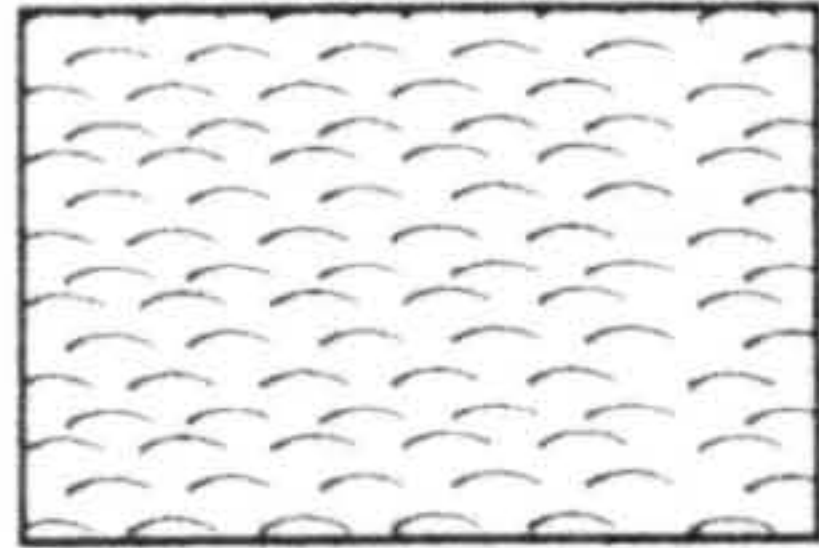
Calcareous Clay



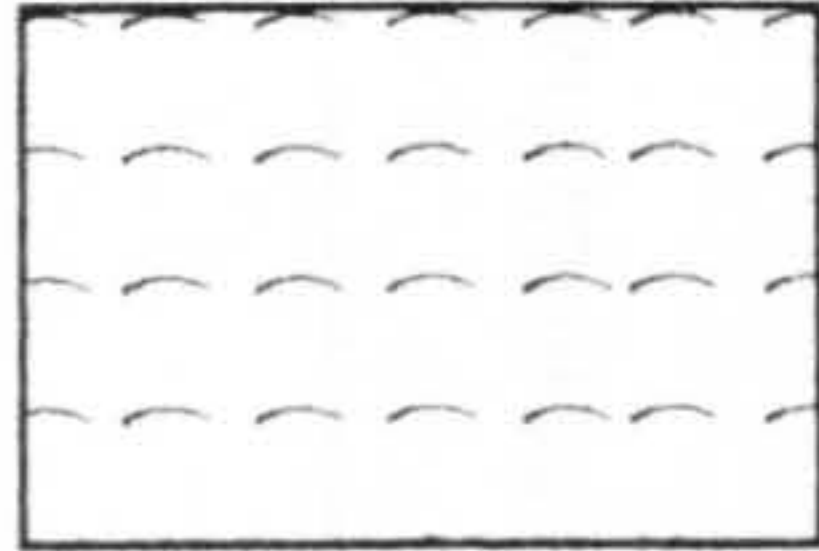
Deposit-feeder Bituminous Shale



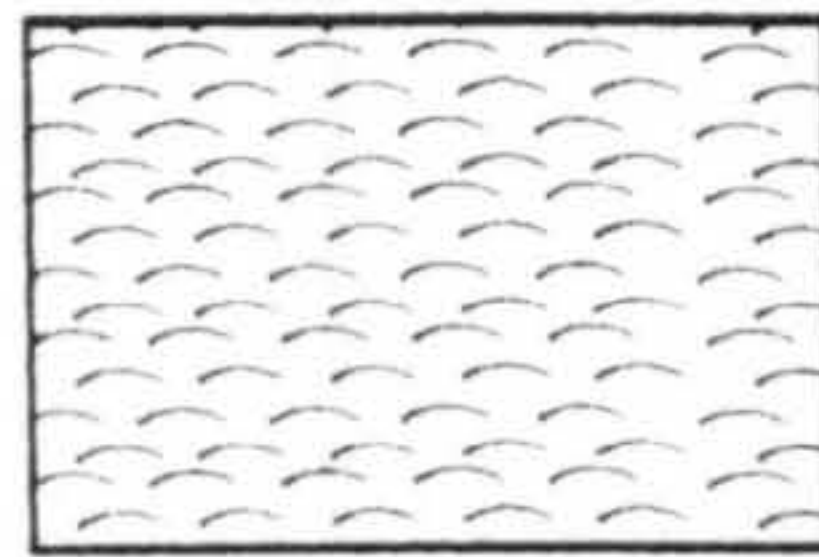
Foraminifera-rich Bituminous Shale



***Grammatodon* Shell Bed**



***Meleagrinnella* Shell Bed**



Nuculacean Shell Bed

Key to facies symbols displayed in Figures 3.4-3.6.

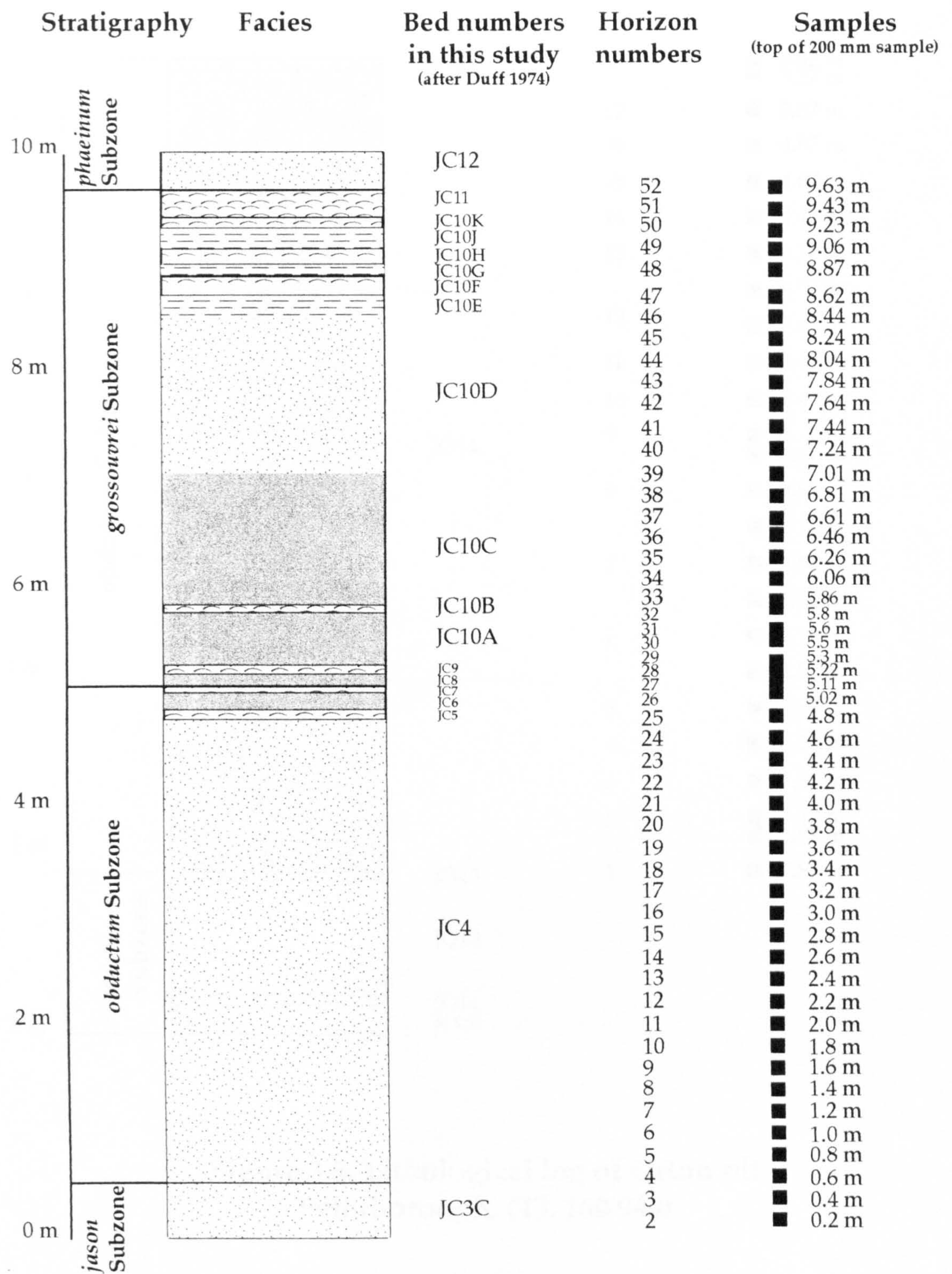


Figure 3.4. Lithological log of Calvert pit, Buckinghamshire, (SP 695 232).

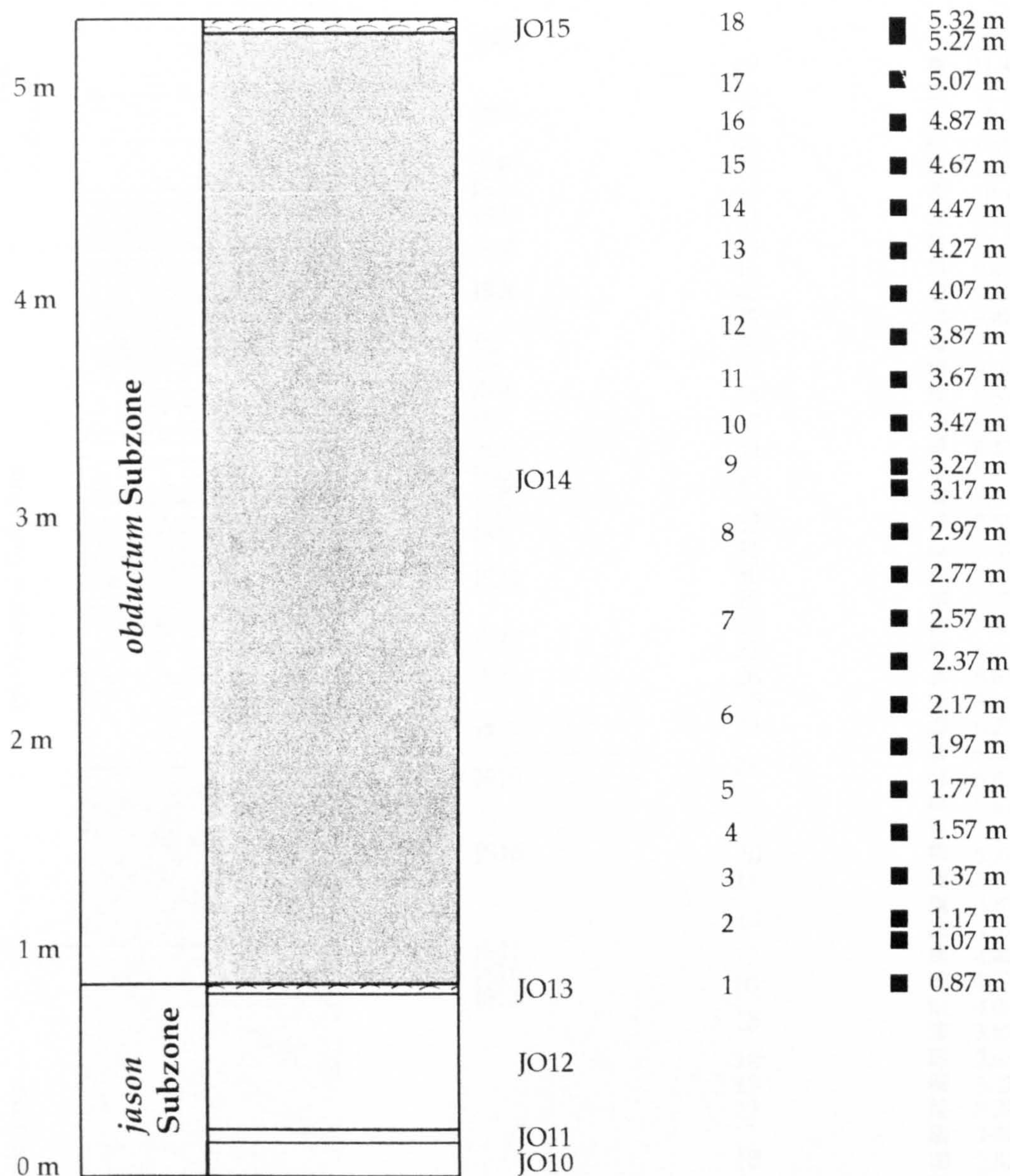


Figure 3.5. Lithological log of Orton pit, Peterborough, (TL 160 940).

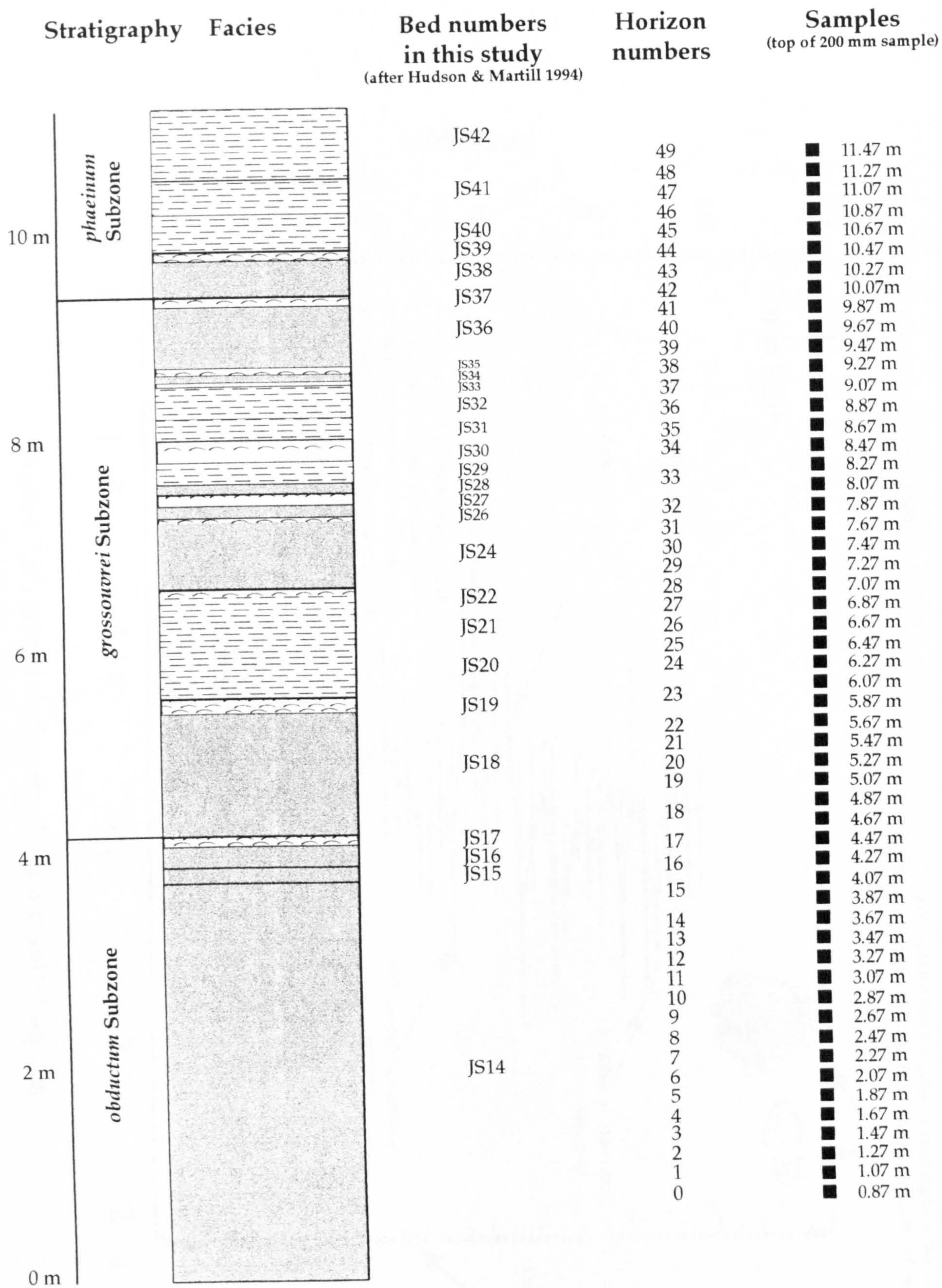


Figure 3.6. Lithological log of Saxon pit, Peterborough, (TL 248 965).

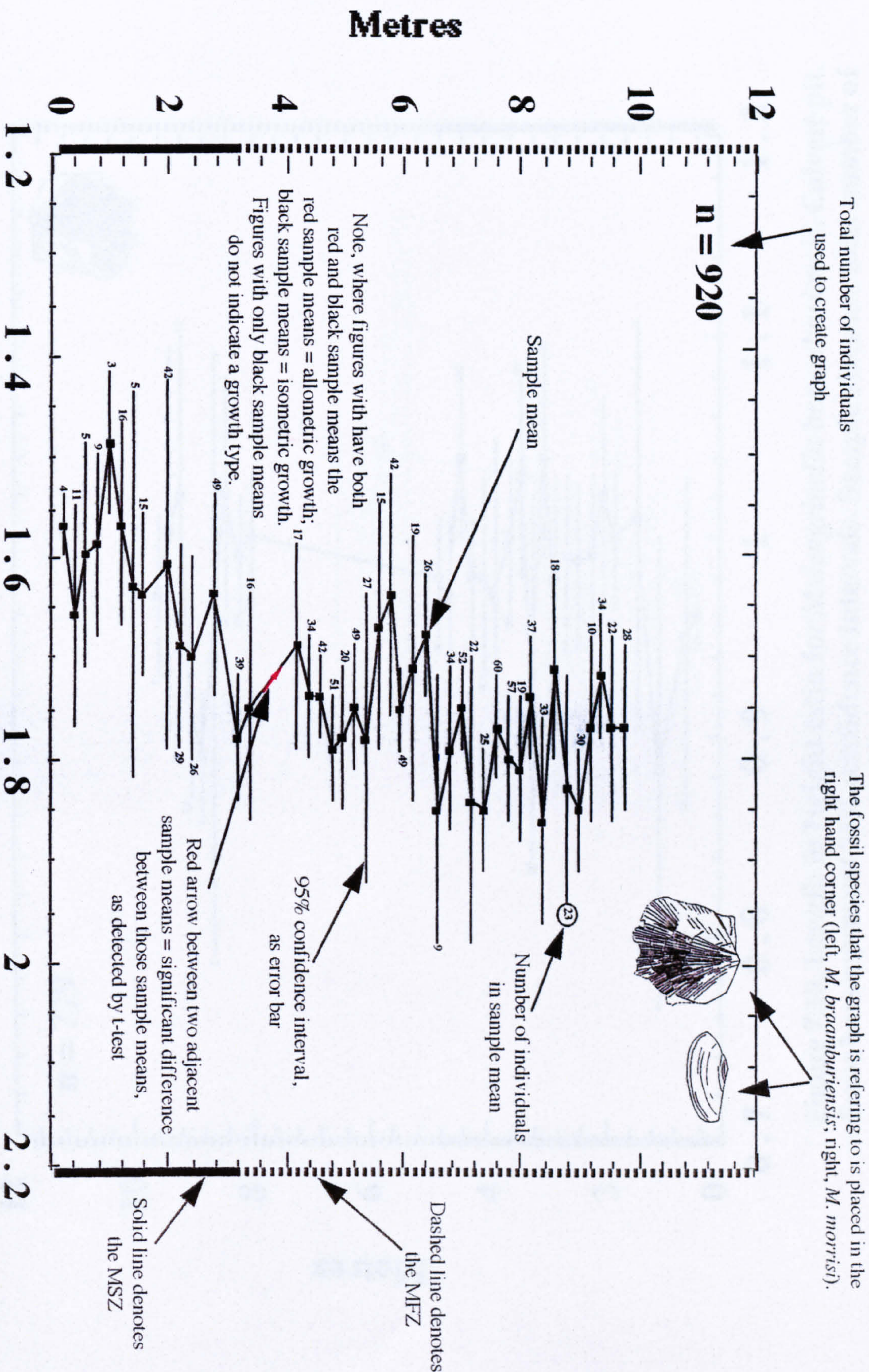


Figure 7.17. Annotated example of a result diagram.

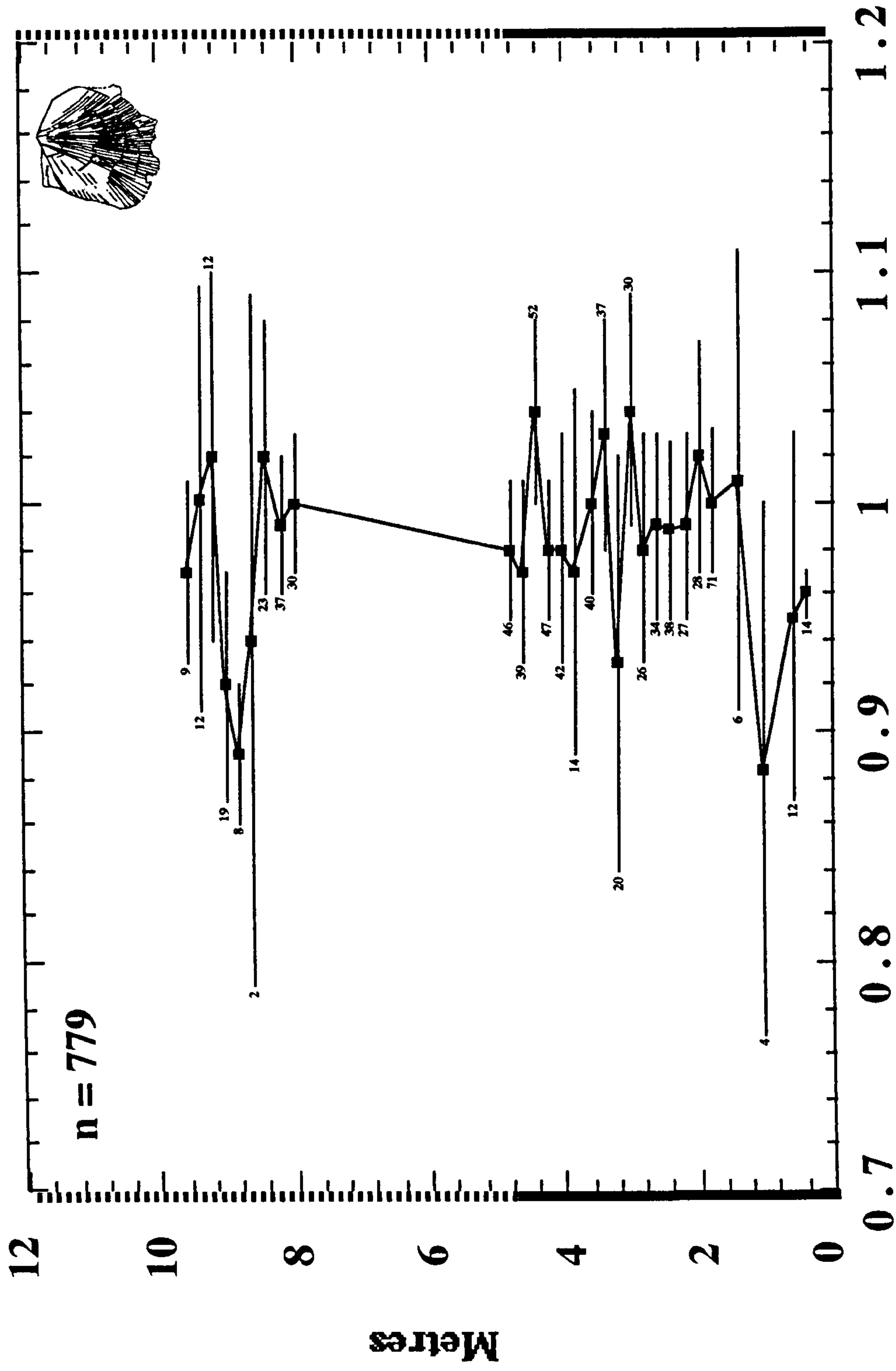


Figure 7.18. Length to Height ratio for *Meleagrionella braamburiensis*, Calvert pit. Error bars represent 95% confidence intervals. Sample sizes are total number of measured individuals for each sample mean.

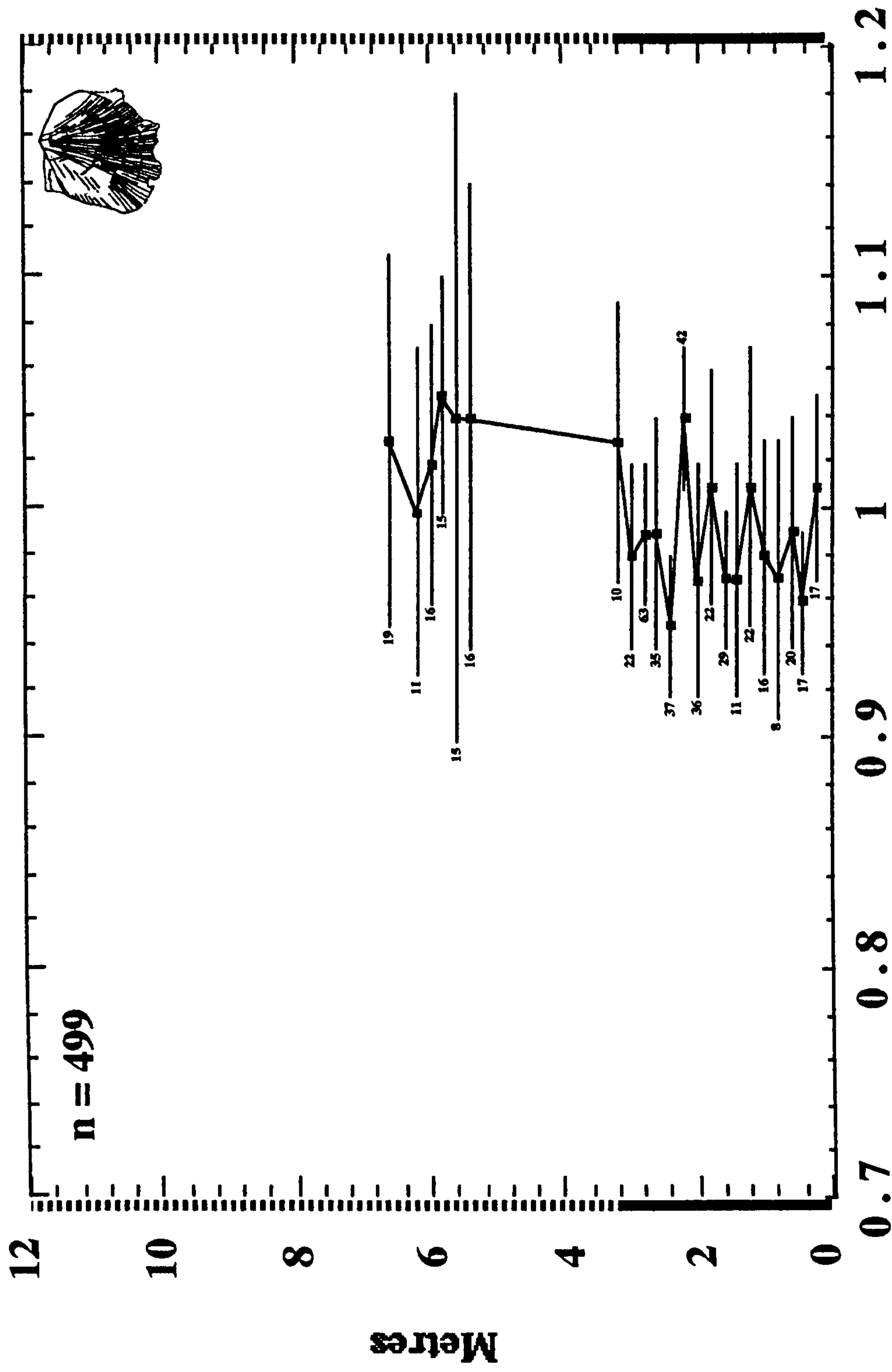


Figure 7.19. Length to Height ratio for *Meleagrinella braamburiensis*, Saxon pit. Error bars represent 95% confidence intervals. Sample sizes are total number of measured individuals for each sample mean.

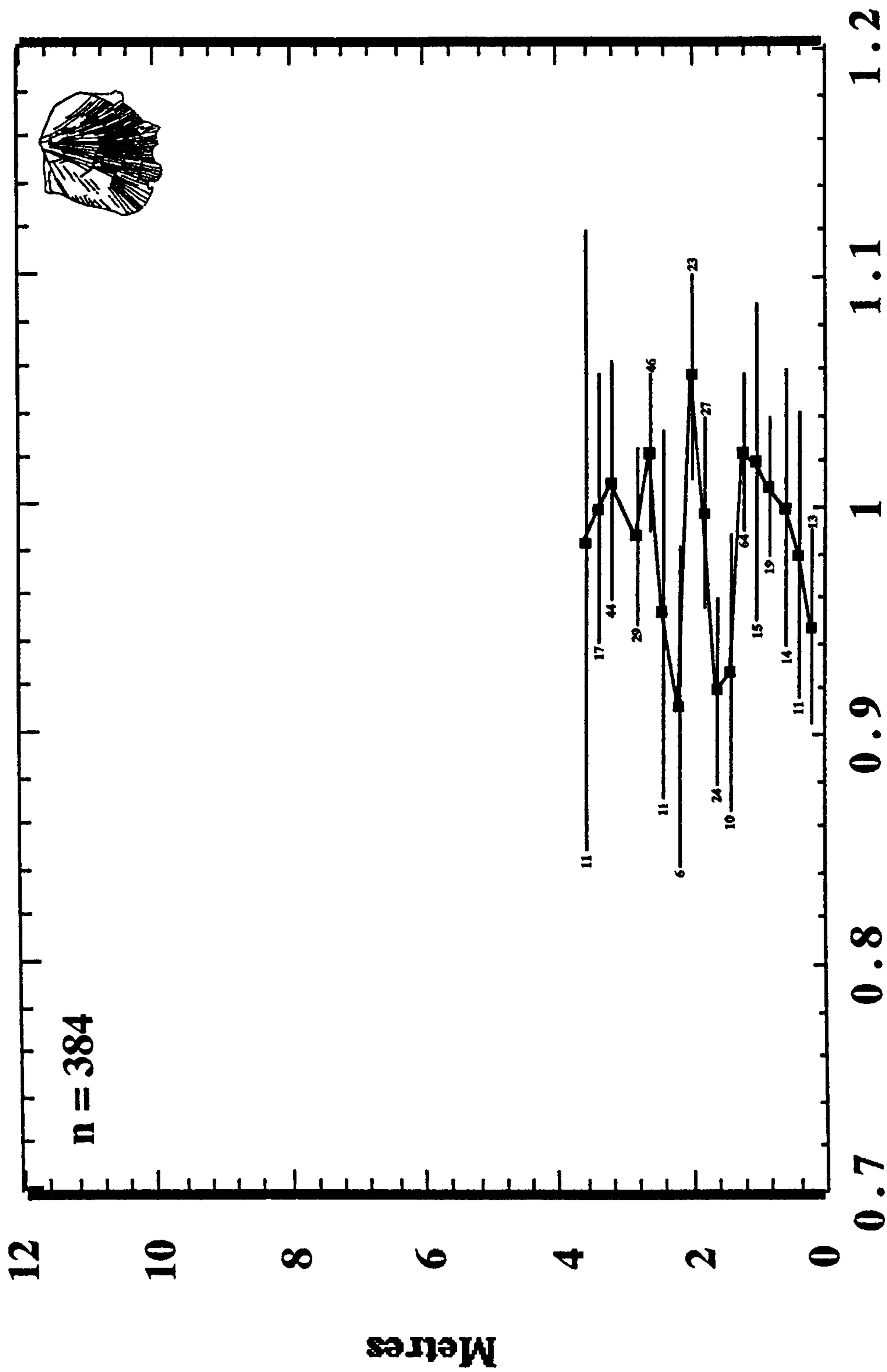


Figure 7.20. Length to Height ratio for *Meleagrinella braamburiensis*, Orton pit. Error bars represent 95% confidence intervals. Sample sizes are total number of measured individuals for each sample mean.

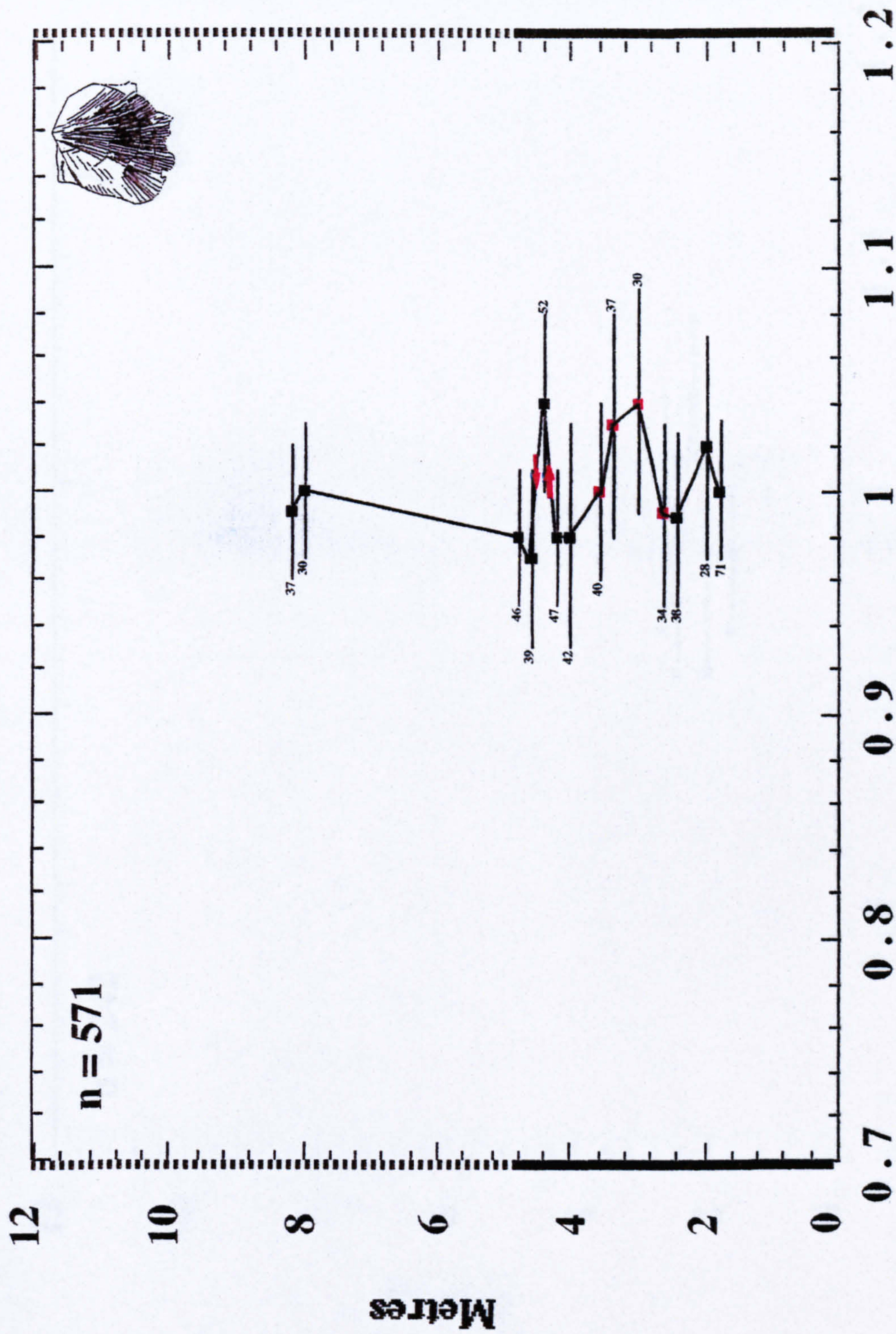


Figure 7.21. Length to Height ratio for *Meleagrionella braamburiensis*, Calvert pit. Error bars represent 95% confidence intervals. Each sample mean = $n > 27$. Black sample means = isometric growth; red sample means = allometric growth. (For all data see Figure 7.18).

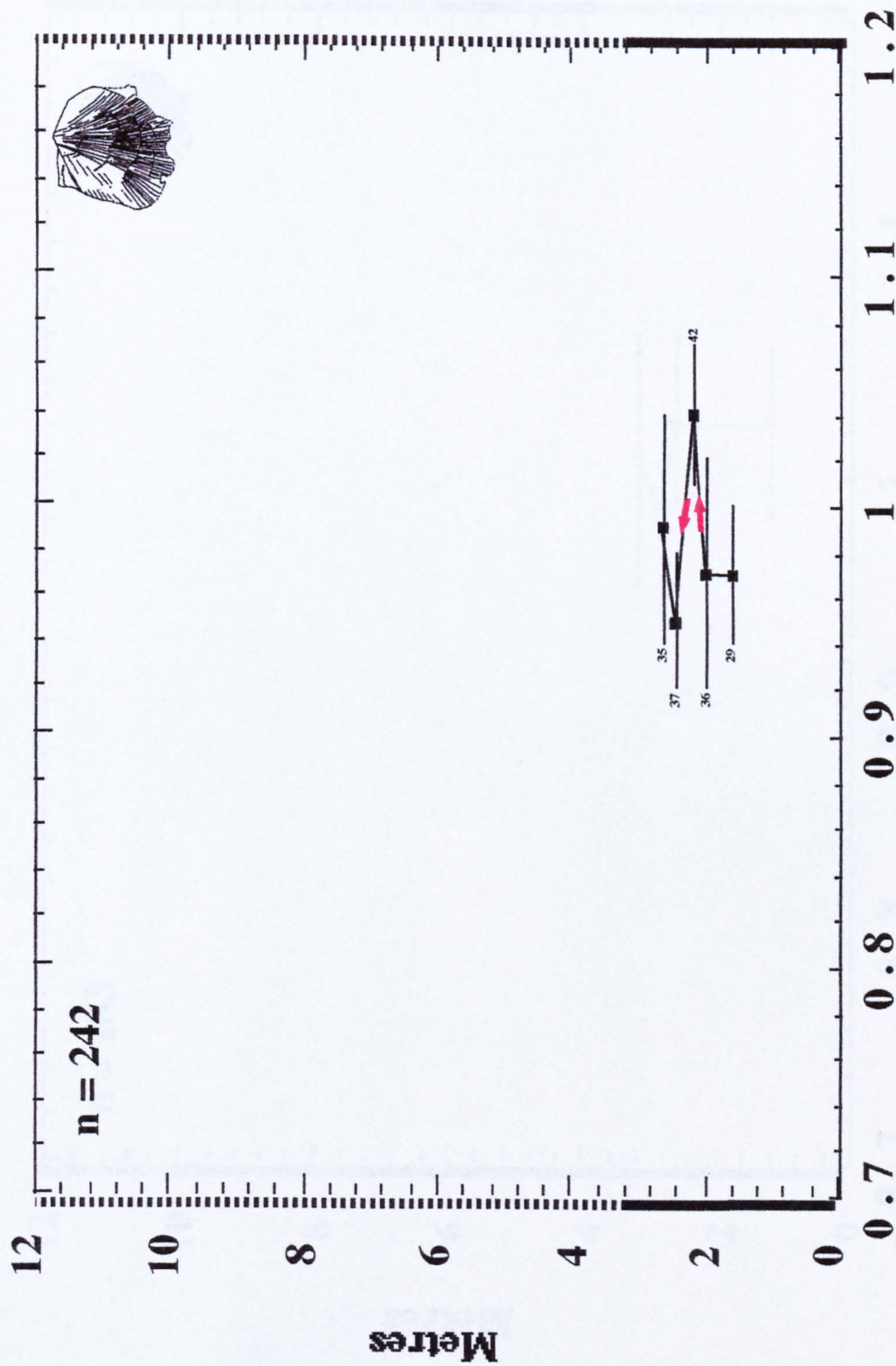


Figure 7.22. Length to Height ratio for *Meleagrionella braamburiensis*, Saxon pit. Error bars represent 95% confidence intervals. Each sample mean = $n > 27$. Black sample means = isometric growth; red sample means = allometric growth. (For all data see Figure 7.19).

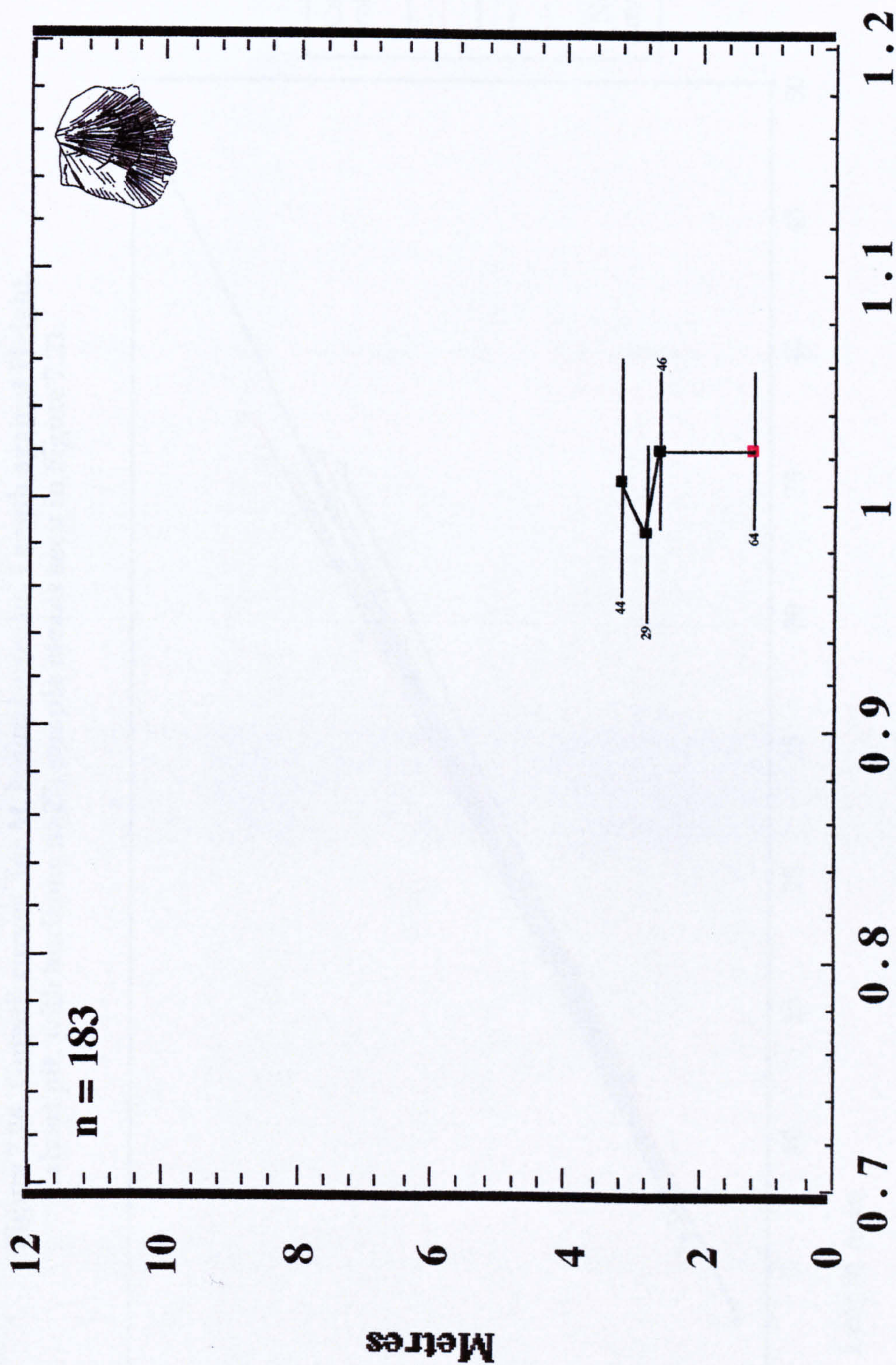


Figure 7.24. Growth curves for *M. braamburiensis*, Length against Height, Calvert pit, with horizons n>27; sample means seen in Figure 7.21.

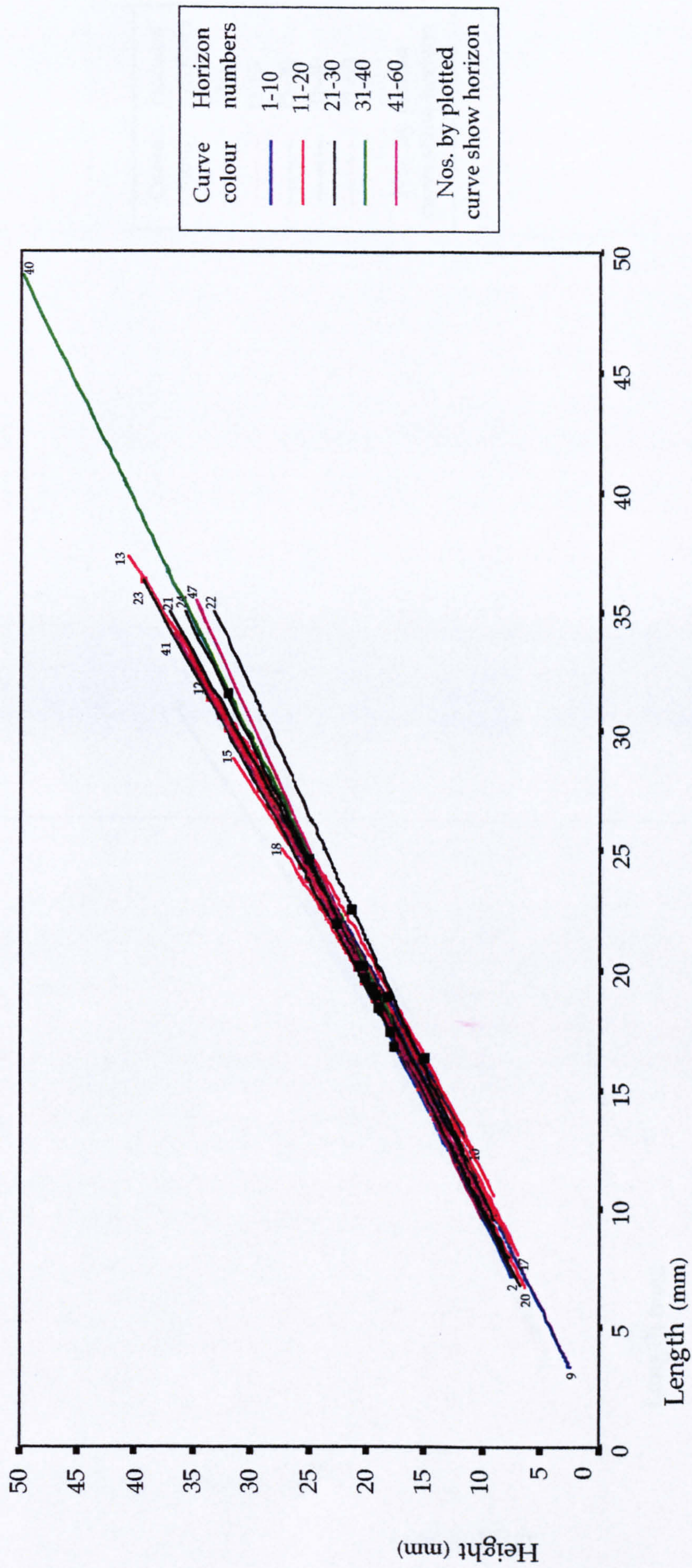


Figure 7.25. Growth curves for *M. braamburiensis*, Length against Height, Saxon pit, with horizons n>14; sample means seen in Figure 7.22.

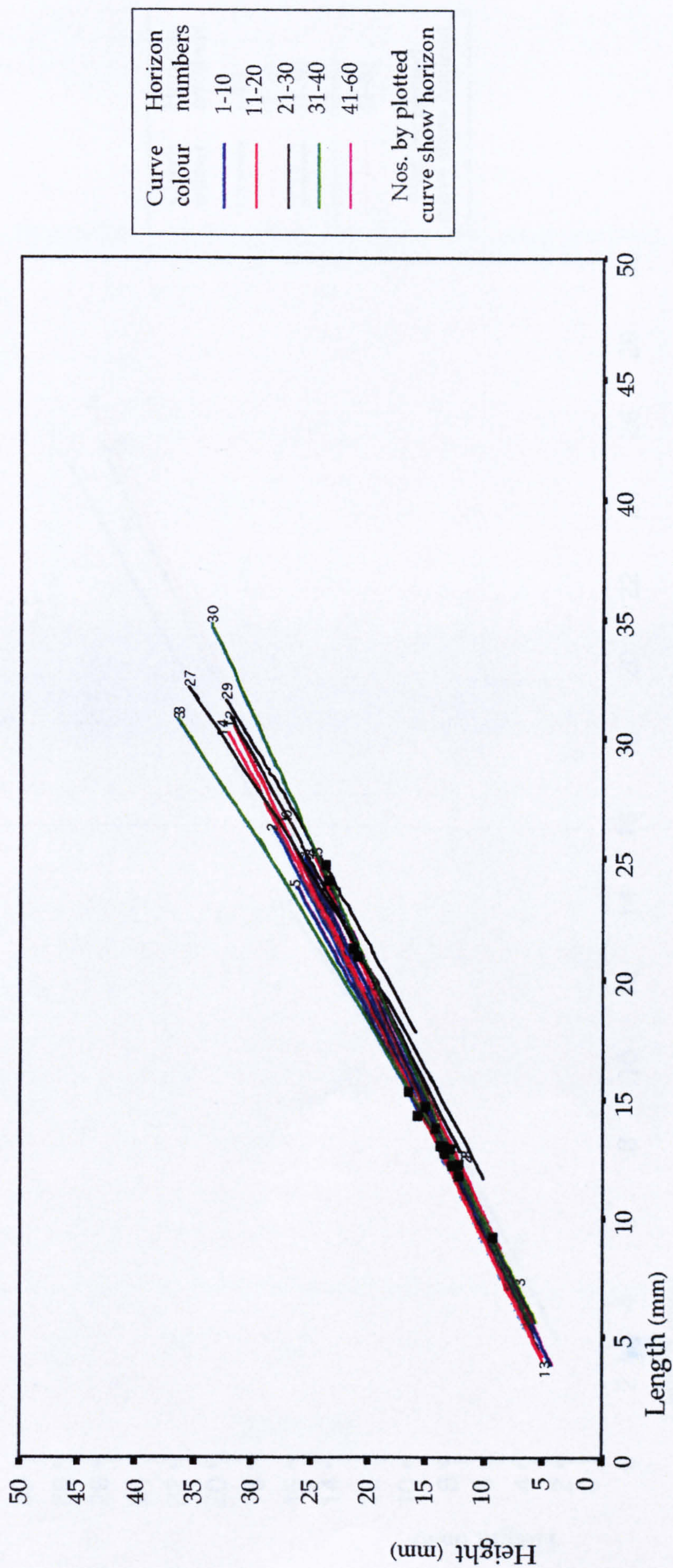
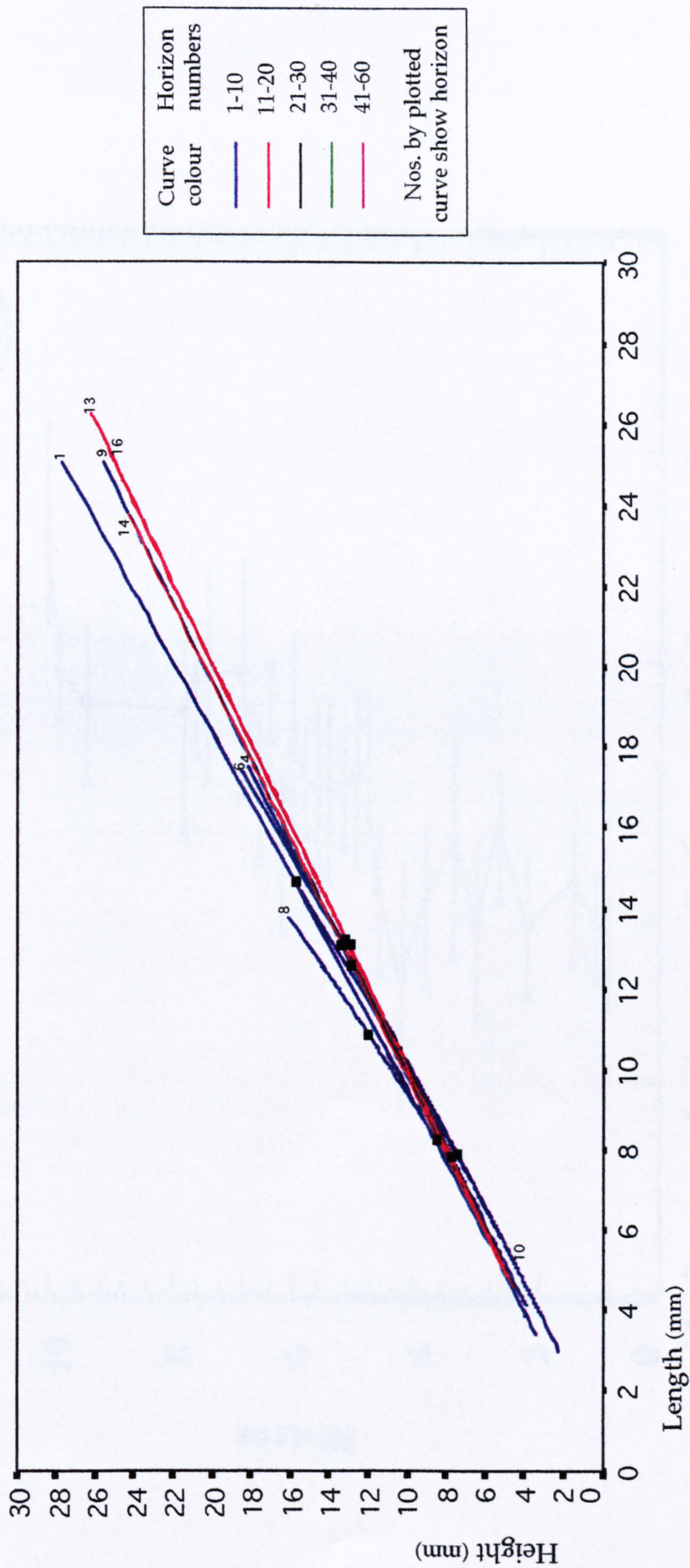


Figure 7.26. Growth curves for *M. braamburiensis*, Length against Height, Orton pit, with horizons n> 12; sample means seen in Figure 7.23.



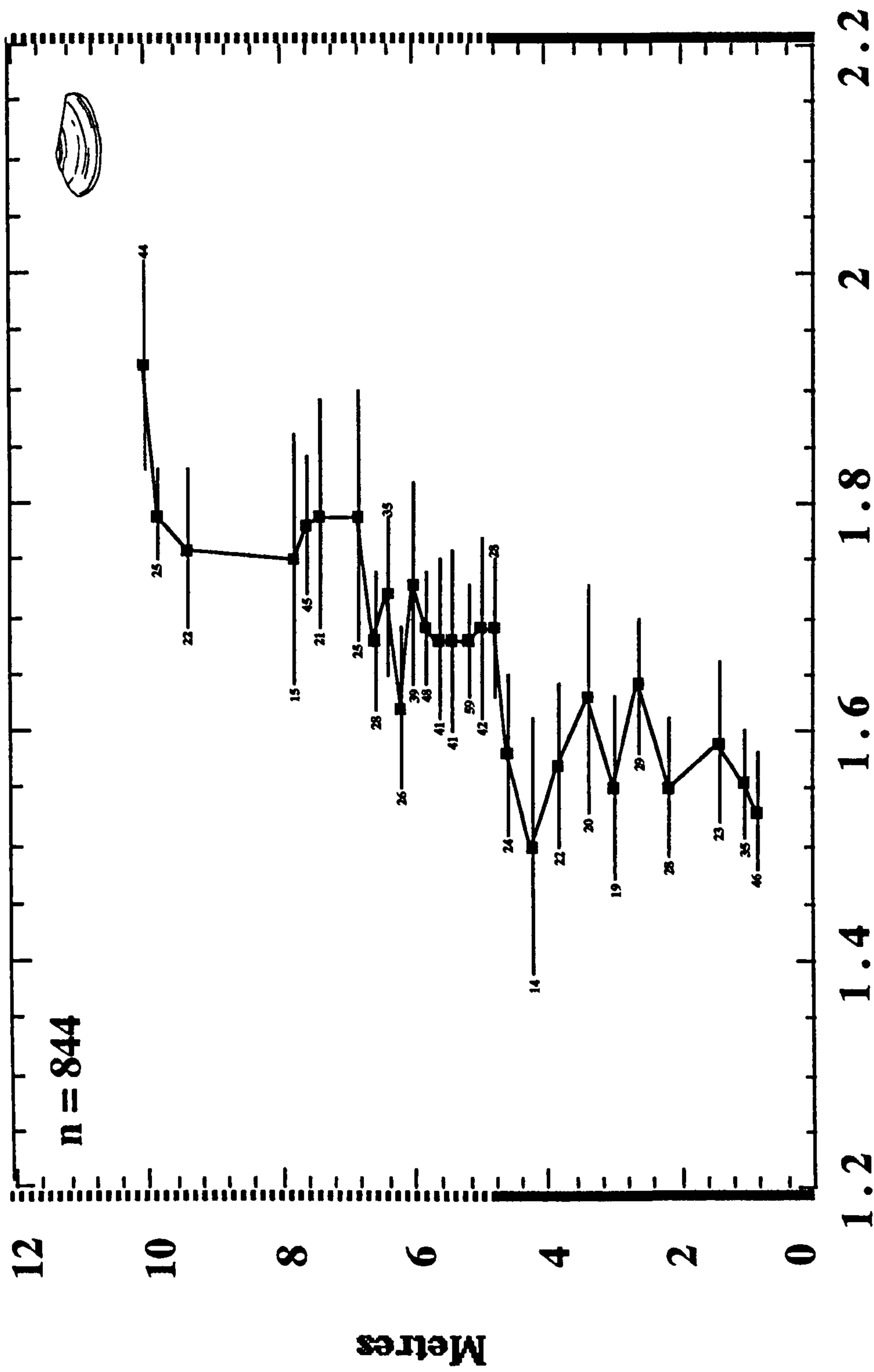


Figure 7.27. Length to Height ratio for *Mesosaccella morrisi*, Calvert pit. Error bars represent 95% confidence intervals. Sample sizes are total number of measured individuals for each sample mean.

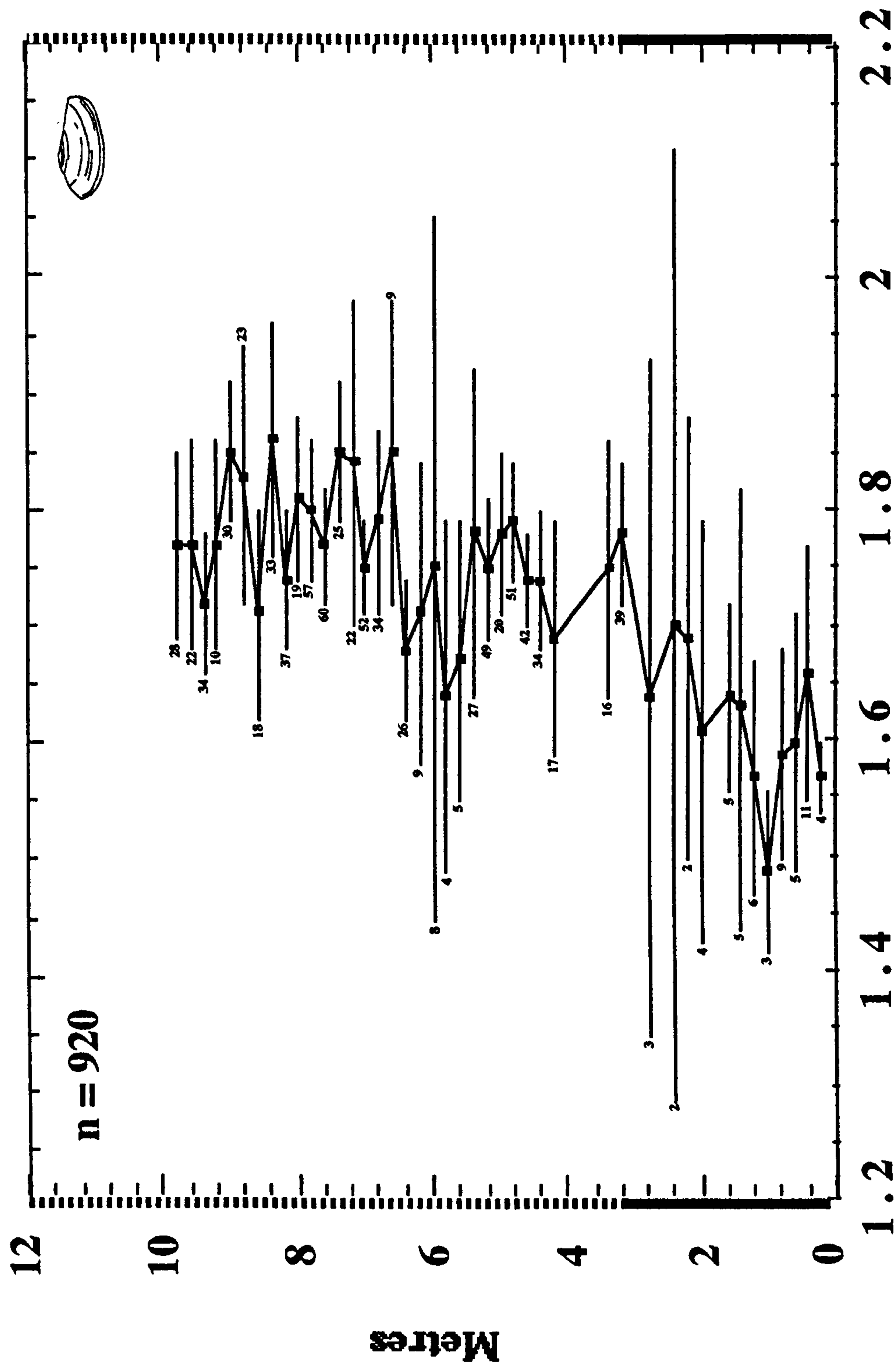


Figure 7.28. Length to Height ratio for *Mesosaccella morrisi*, Saxon pit. Error bars represent 95% confidence intervals. Sample sizes are total number of measured individuals for each sample mean.

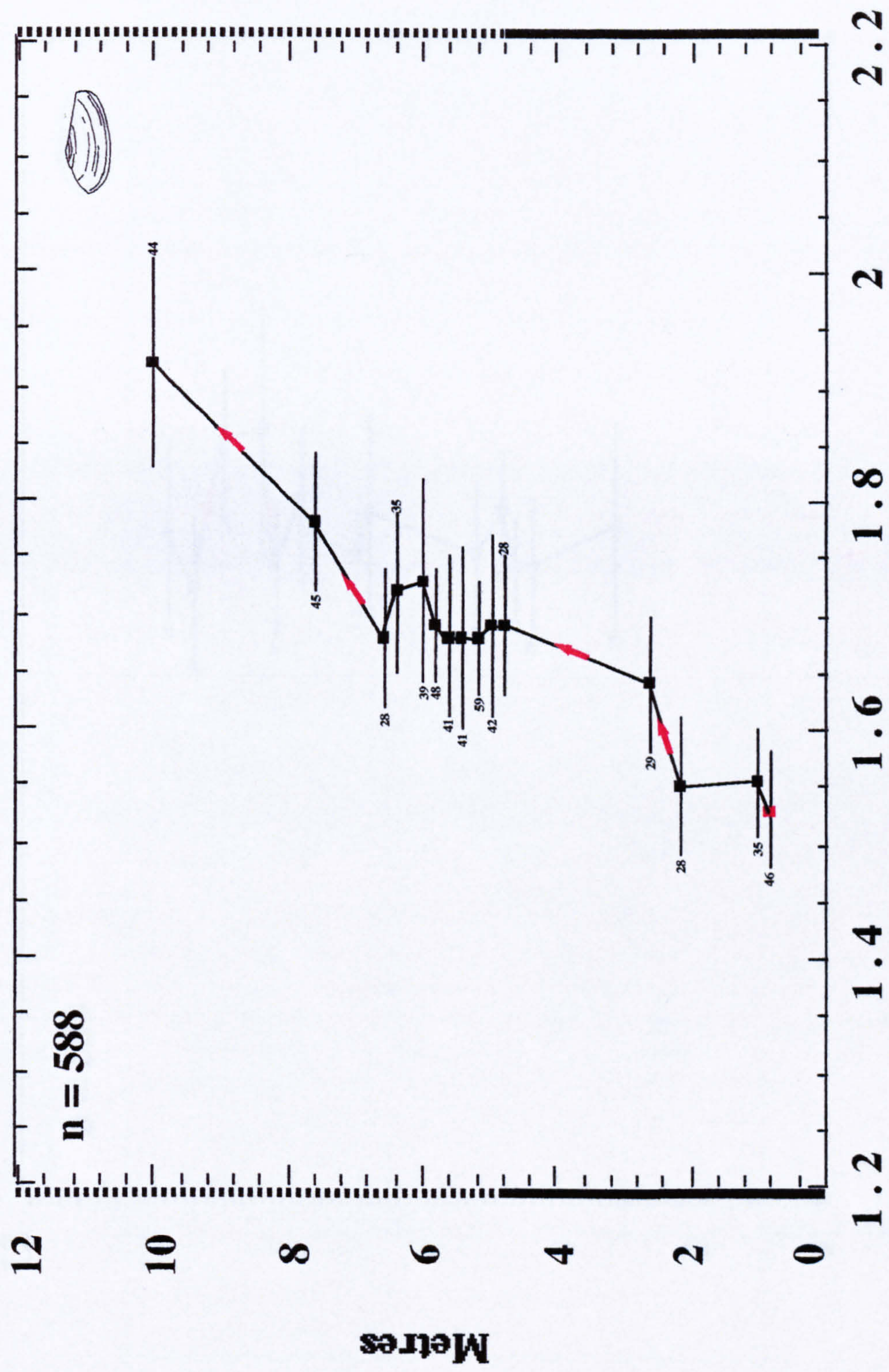


Figure 7.29. Length to Height ratio for *Mesosaccella morrisi*, Calvert pit. Error bars represent 95% confidence intervals. Each sample mean = $n > 27$. Black sample means = isometric growth; red sample means = allometric growth. (For all data see Figure 7.27).

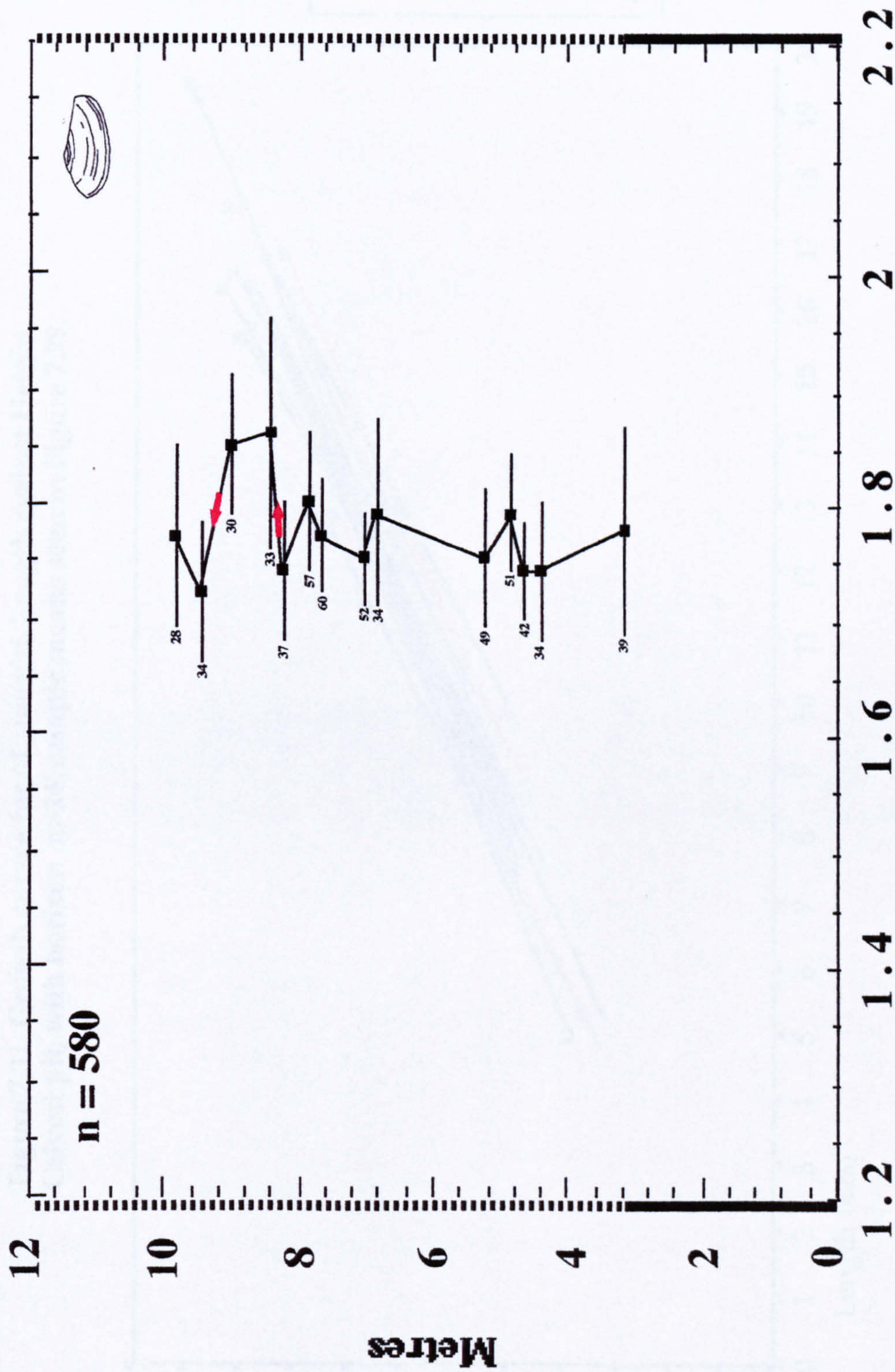


Figure 7.30. Length to Height ratio for *Mesosaccella morrisi*, Saxon pit. Error bars represent 95% confidence intervals. Each sample mean = $n > 27$. Black sample means = isometric growth; red sample means = allometric growth. (For all data see Figure 7.28).

Figure 7.31. Growth curves for *M. morrisi*, Length against Height, Calvert pit, with horizon n>24; sample means seen in Figure 7.29.

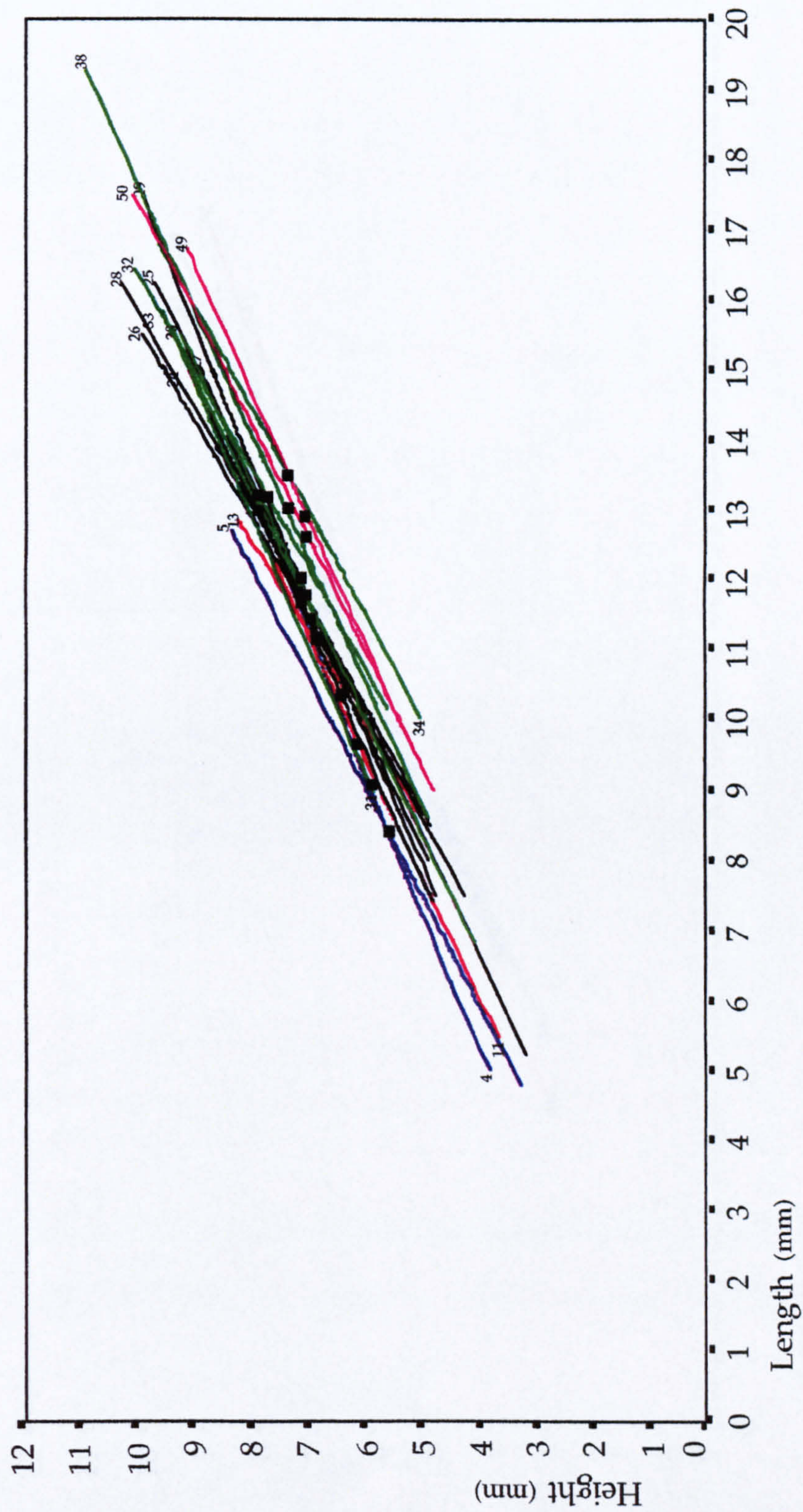
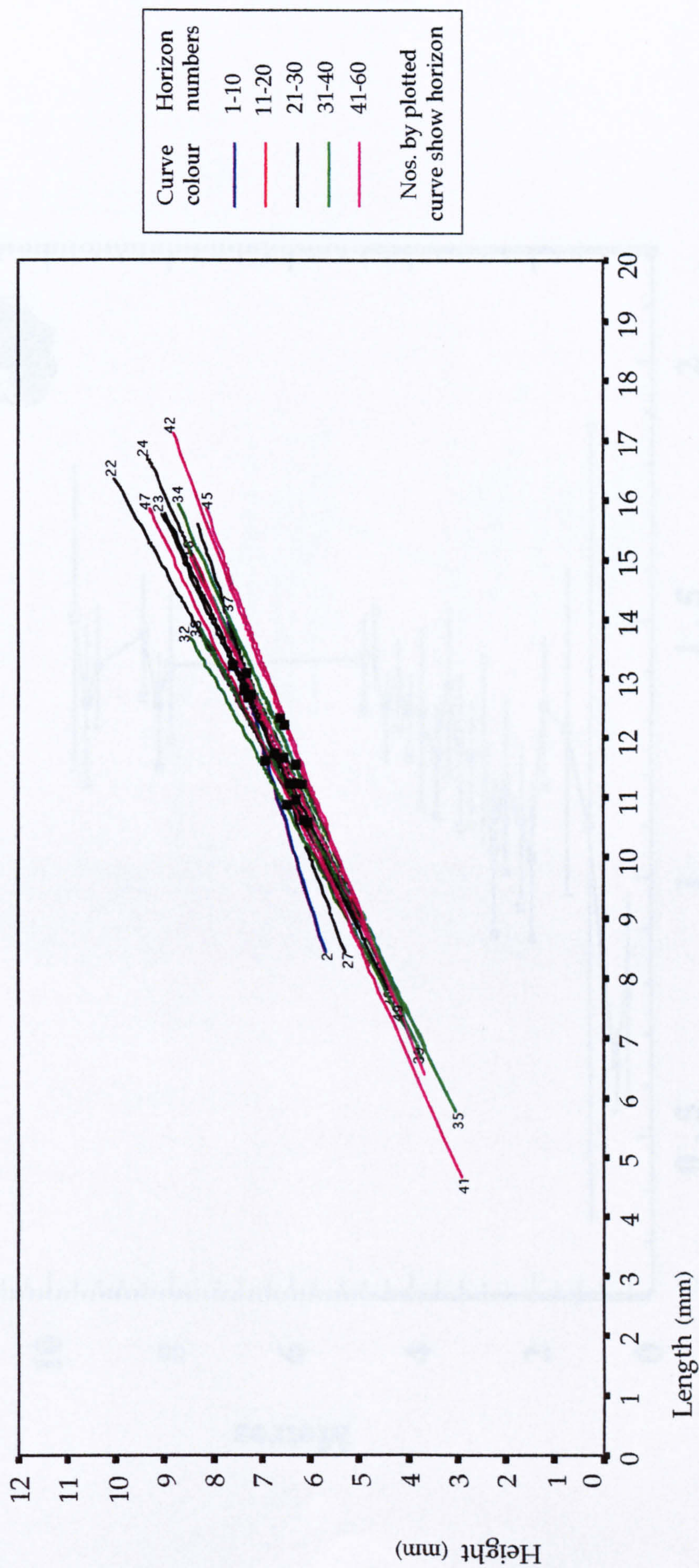


Figure 7.32. Growth curves for *M. morrisi*, Length against Height, Saxon pit, with horizons n>24; sample means seen in Figure 7.30



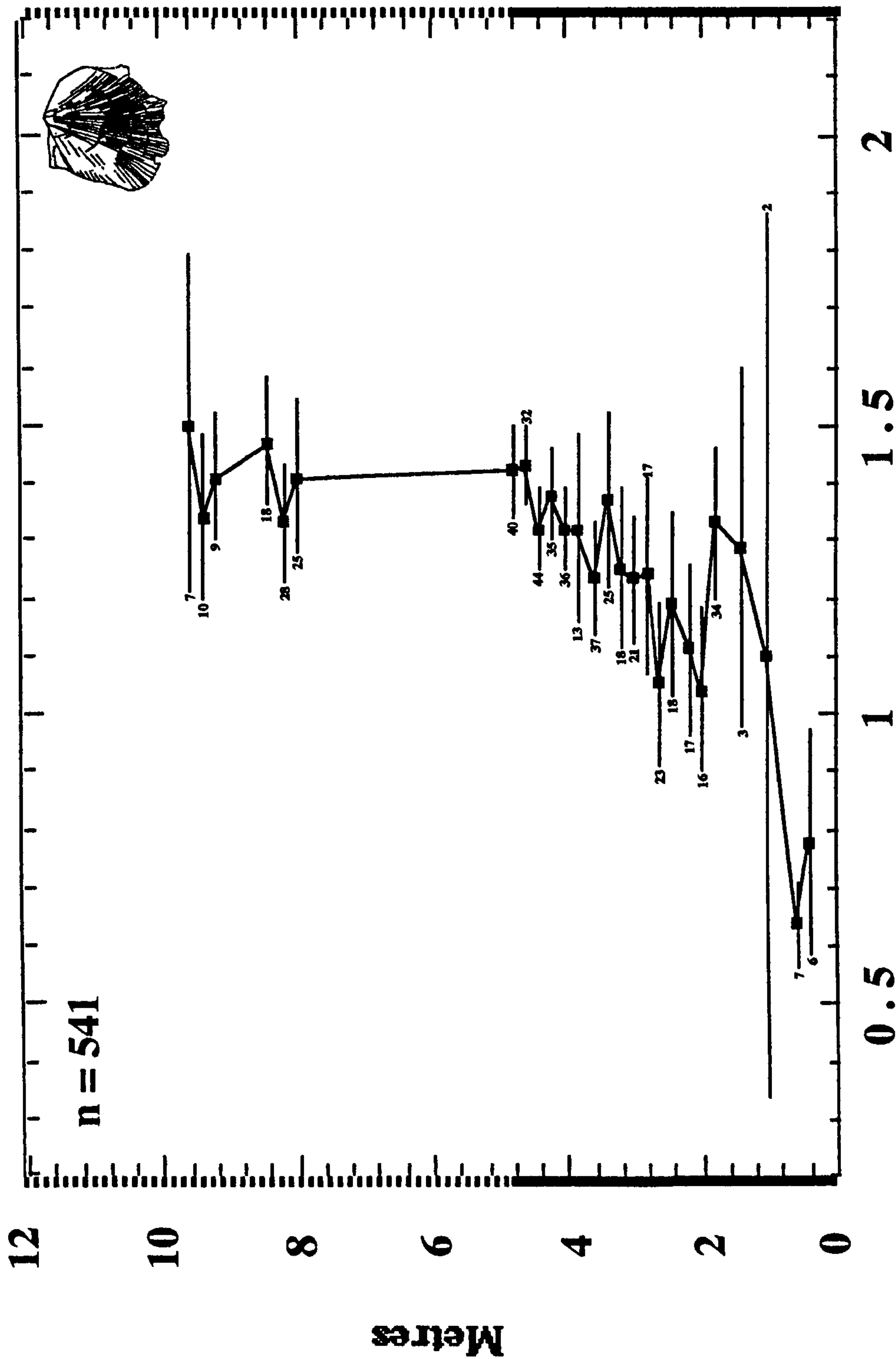


Figure 7.33. Hinge Length to Anterior Length ratio for *Meleagrinerella braamburiensis*, Calvert Pit. Error bars represent 95% confidence intervals. Sample sizes are total number of measured individuals for each sample mean.

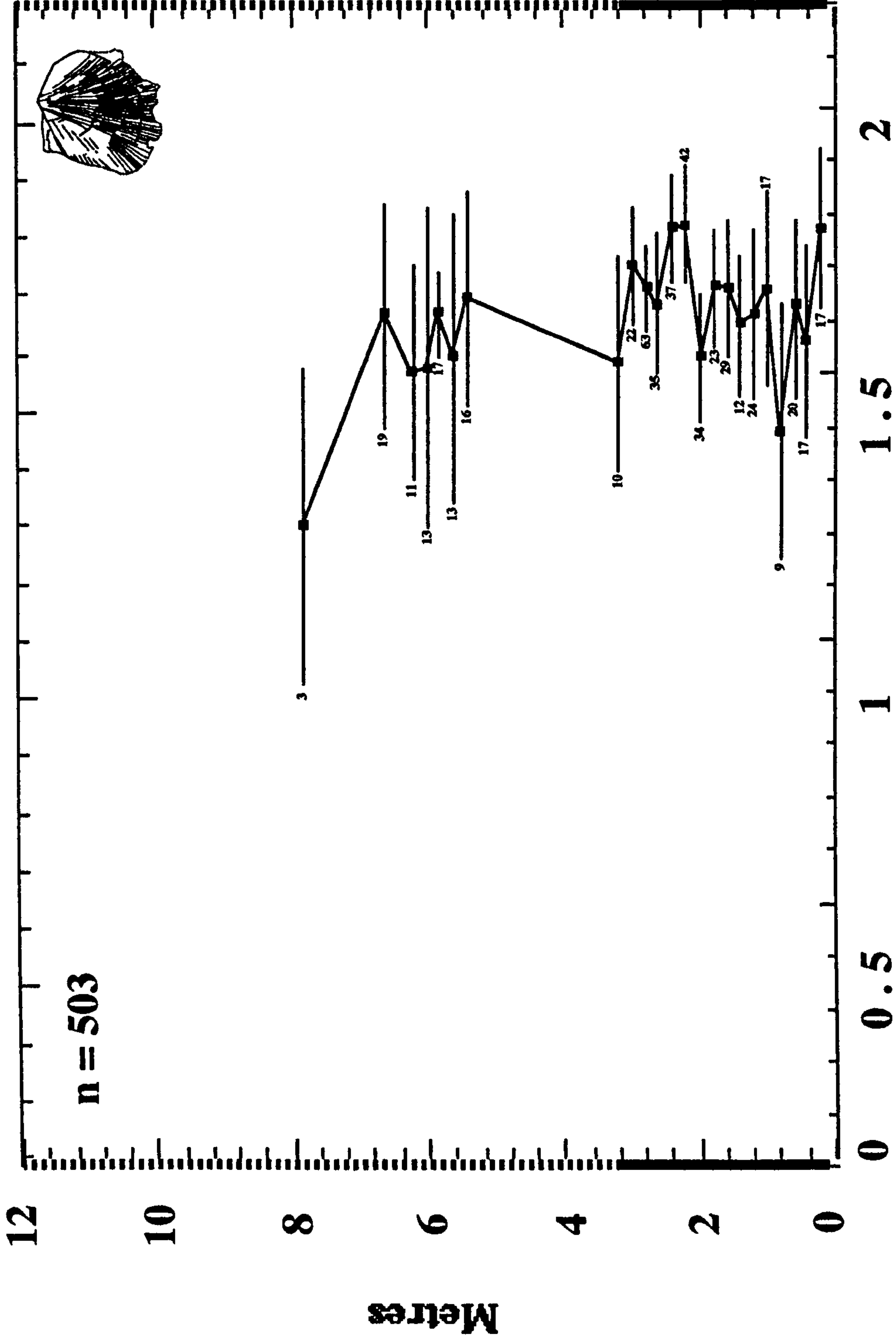


Figure 7.34. Hinge Length to Anterior Length ratio for *Meleagrinnella braamburiensis*, Saxon pit. Error bars represent 95% confidence intervals. Sample sizes are total number of measured individuals for each sample mean.

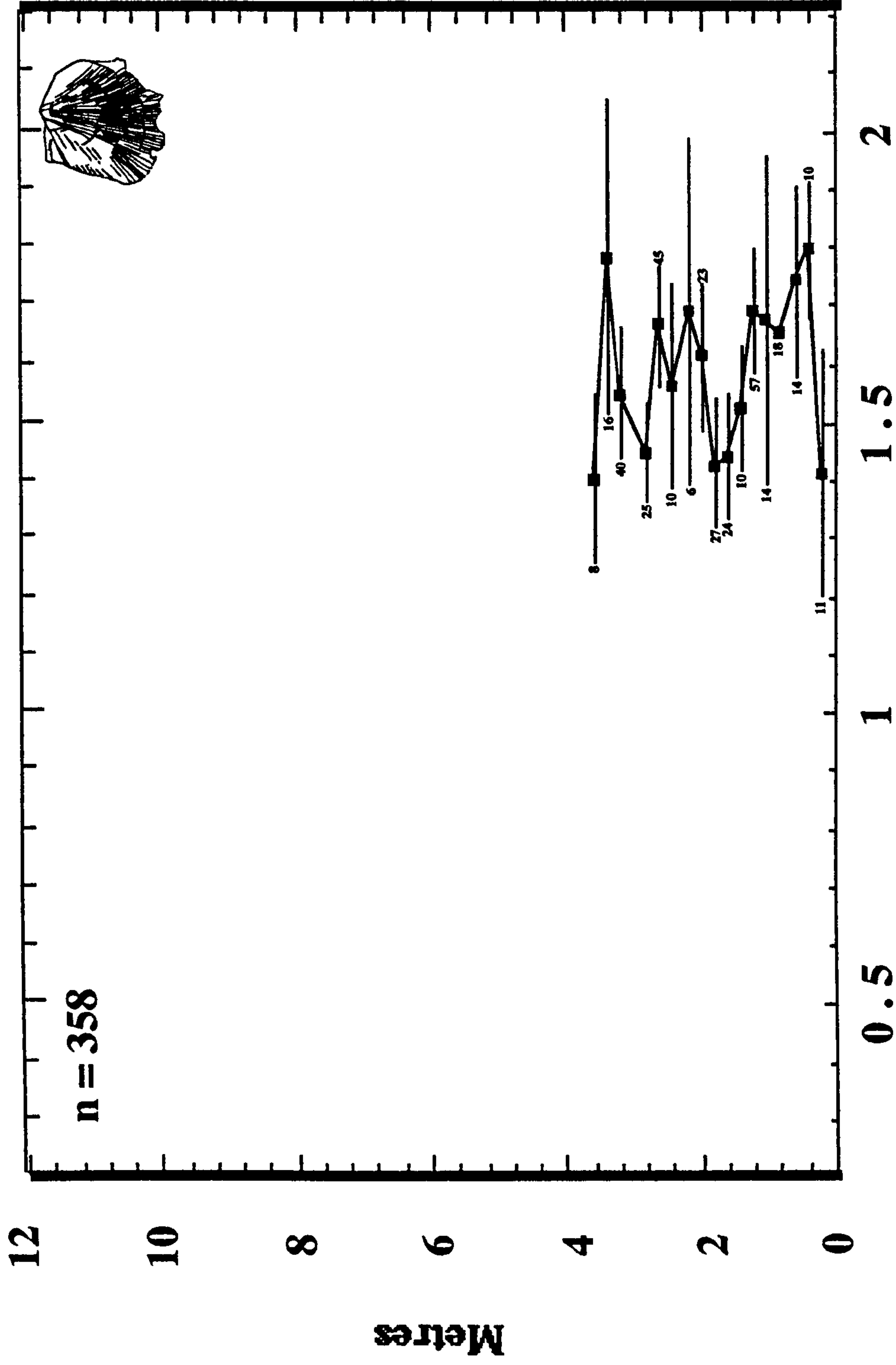


Figure 7.35. Hinge Length to Anterior Length ratio for *Meleagrinerella braamburiensis*, Orton pit. Error bars represent 95% confidence intervals. Sample sizes are total number of measured individuals for each sample mean.

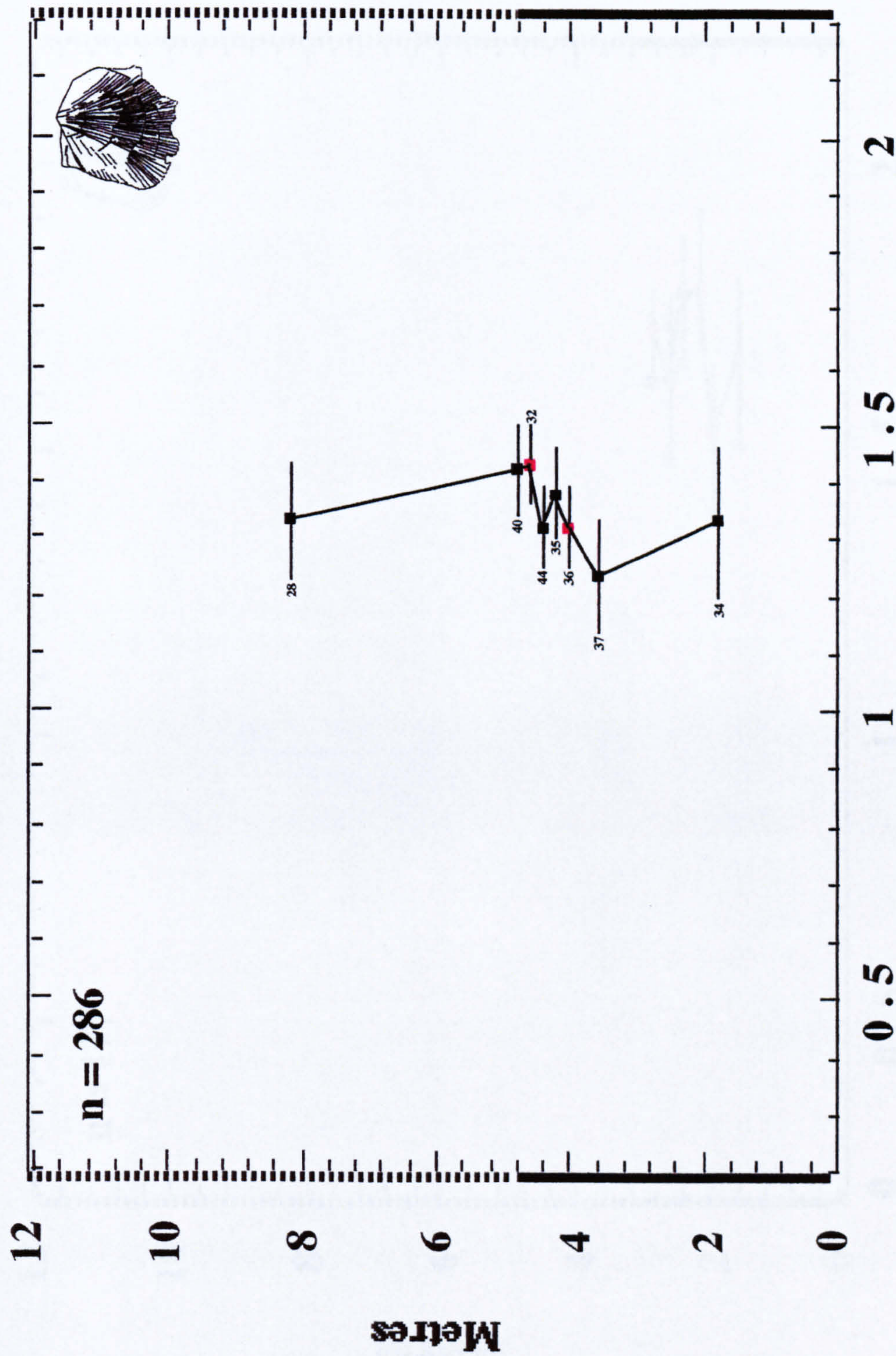


Figure 7.36. Hinge Length to Anterior Length ratio for *Meleagrionella braamburiensis*, Calvert pit. Error bars represent 95% confidence intervals. Each sample mean = $n > 27$. Black sample means = isometric growth; red sample means = allometric growth. (For all data see Figure 7.33).

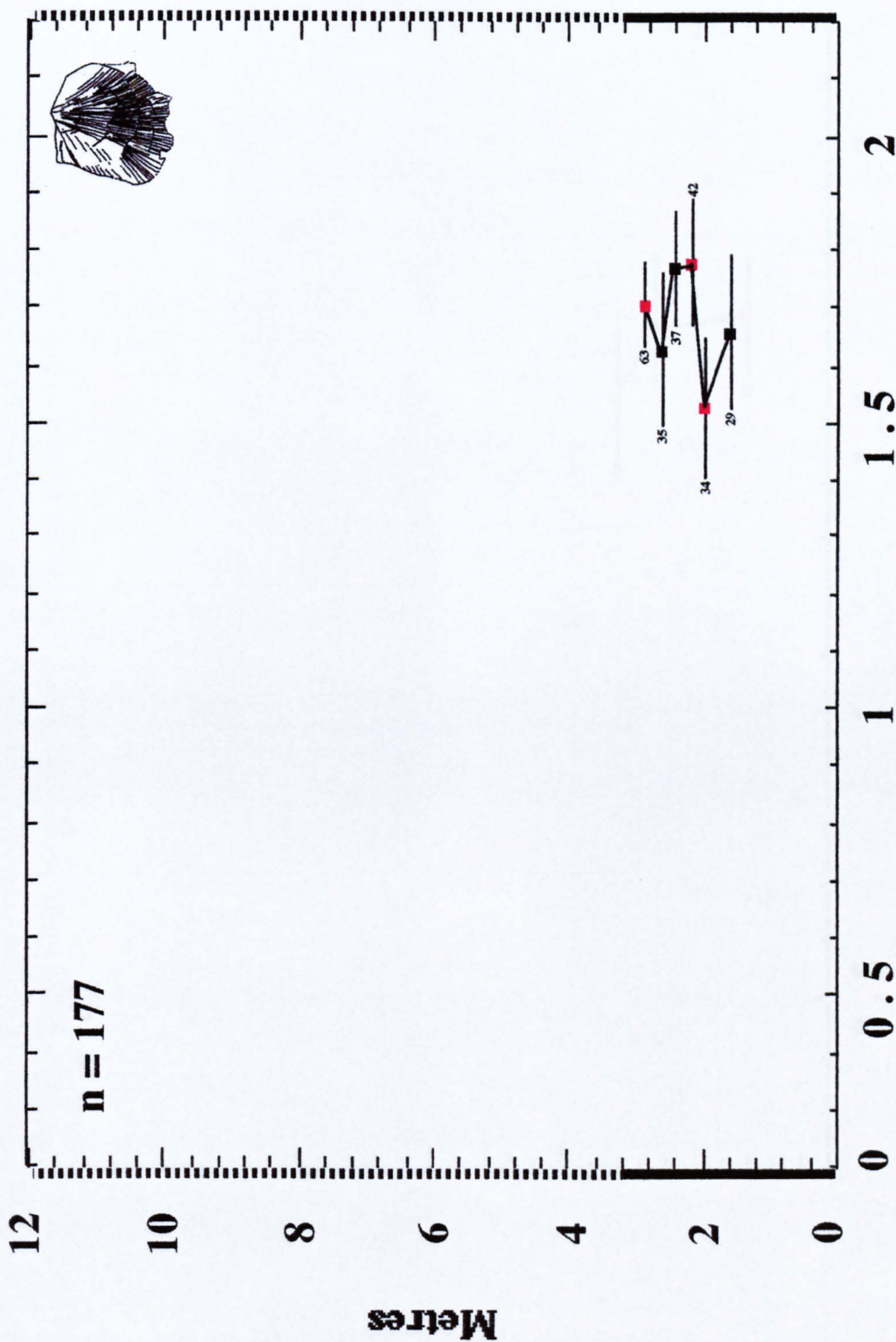


Figure 7.37. Hinge Length to Anterior Length ratio for *Meleagrinnella braamburiensis*, Saxon pit. Error bars represent 95% confidence intervals. Each sample mean = $n > 27$. Black sample means = isometric growth; red sample means = allometric growth. (For all data see Figure 7.34).

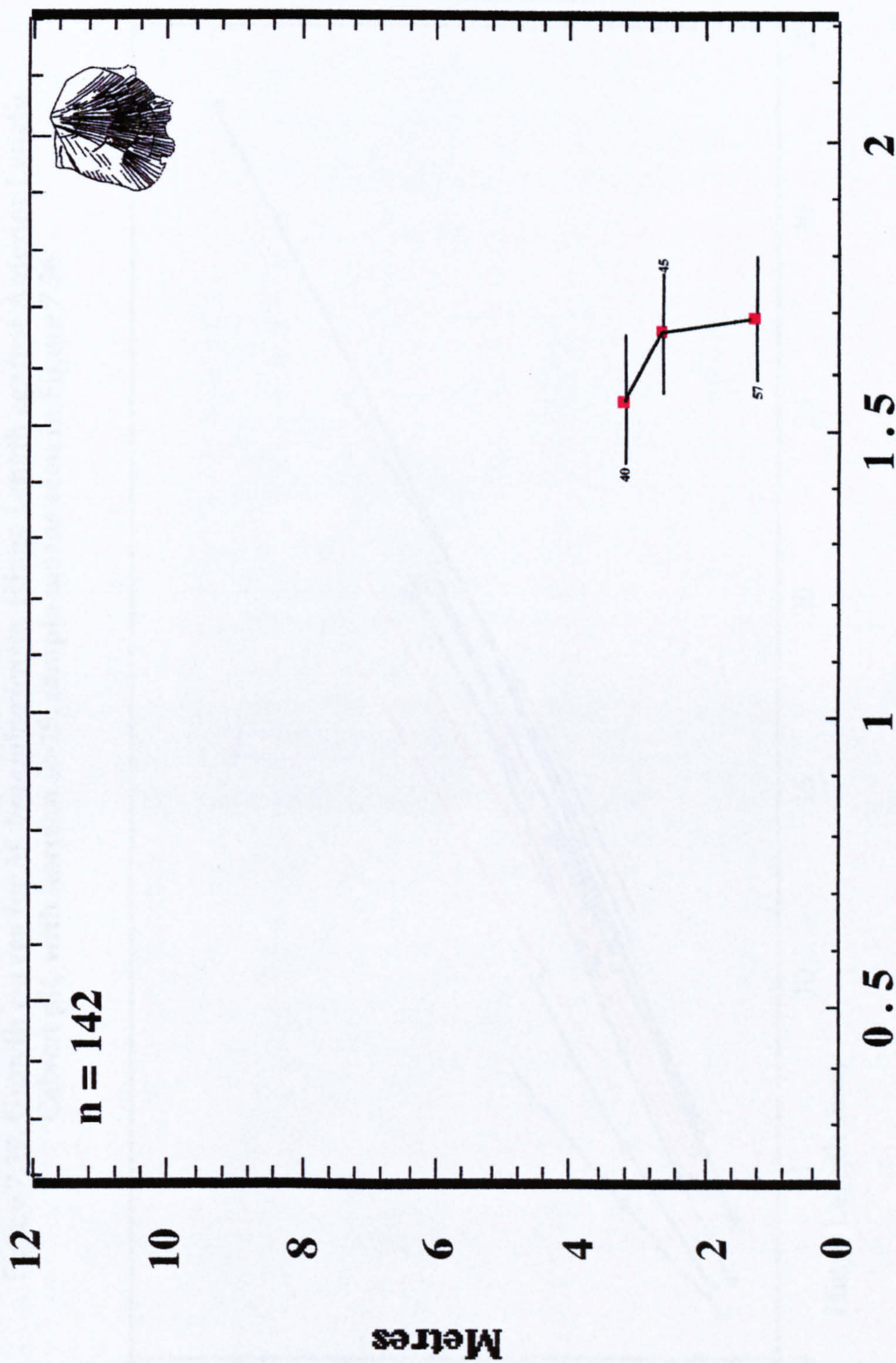


Figure 7.38. Hinge Length to Anterior Length ratio for *Meleagrinnella braamburiensis*, Orton pit. Error bars represent 95% confidence intervals. Each sample mean = $n > 27$. Black sample means = isometric growth; red sample means = allometric growth. (For all data see Figure 7.35).

Figure 7.39. Growth curves for *M. braamburiensis*, Hinge Length against Anterior Length, Calvert pit, with horizon n>15; sample means seen in Figure 7.36.

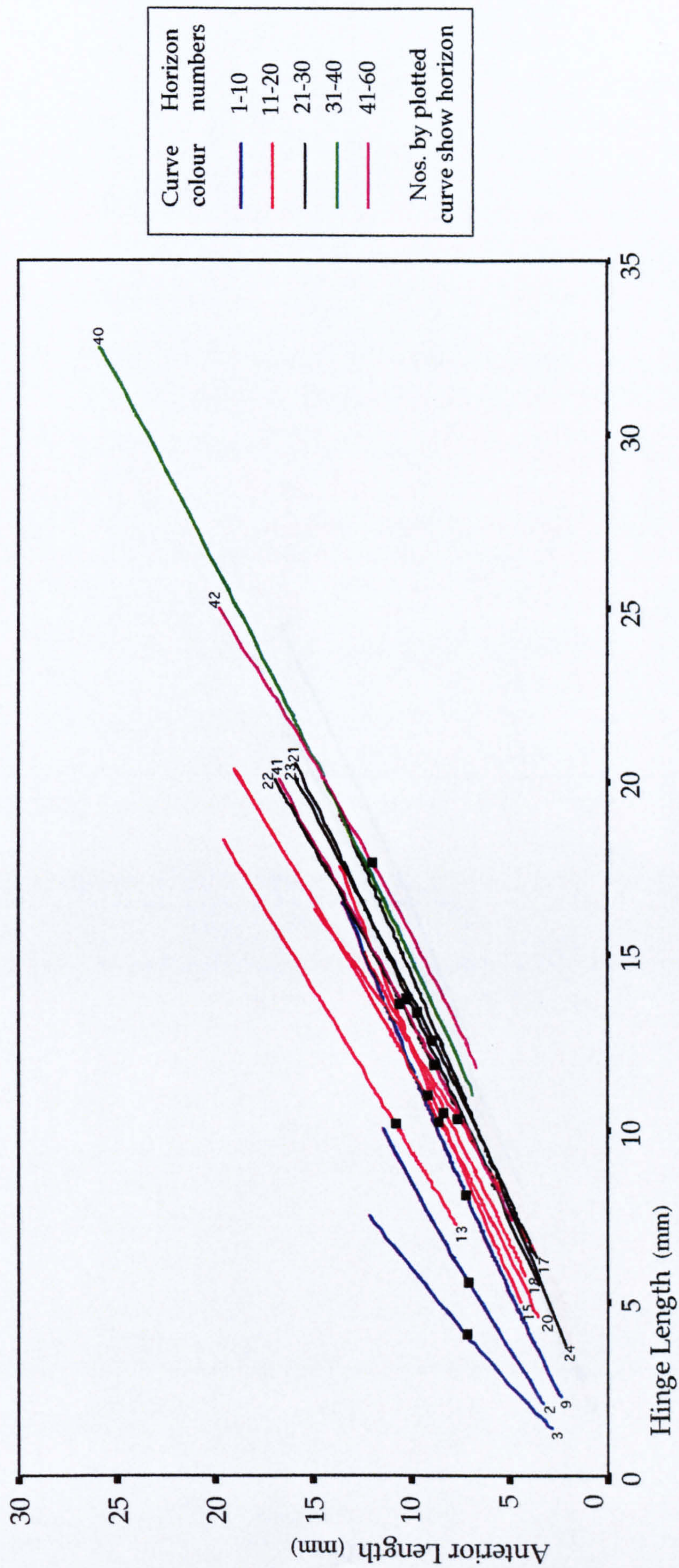


Figure 7.40. Growth curves for *M. braamburiensis*, Hinge Length against Anterior Length, Saxon pit, with horizon n>15; sample means seen in Figure 7.37.

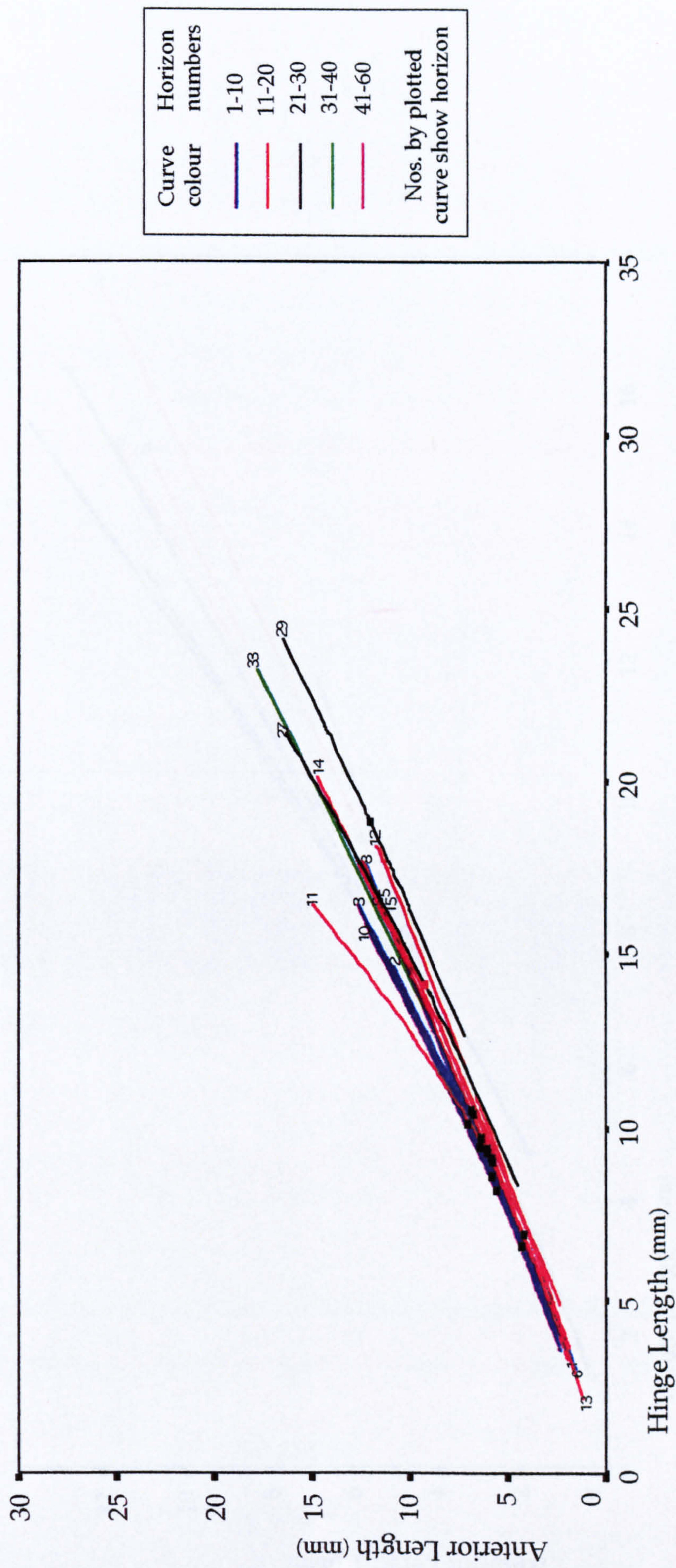
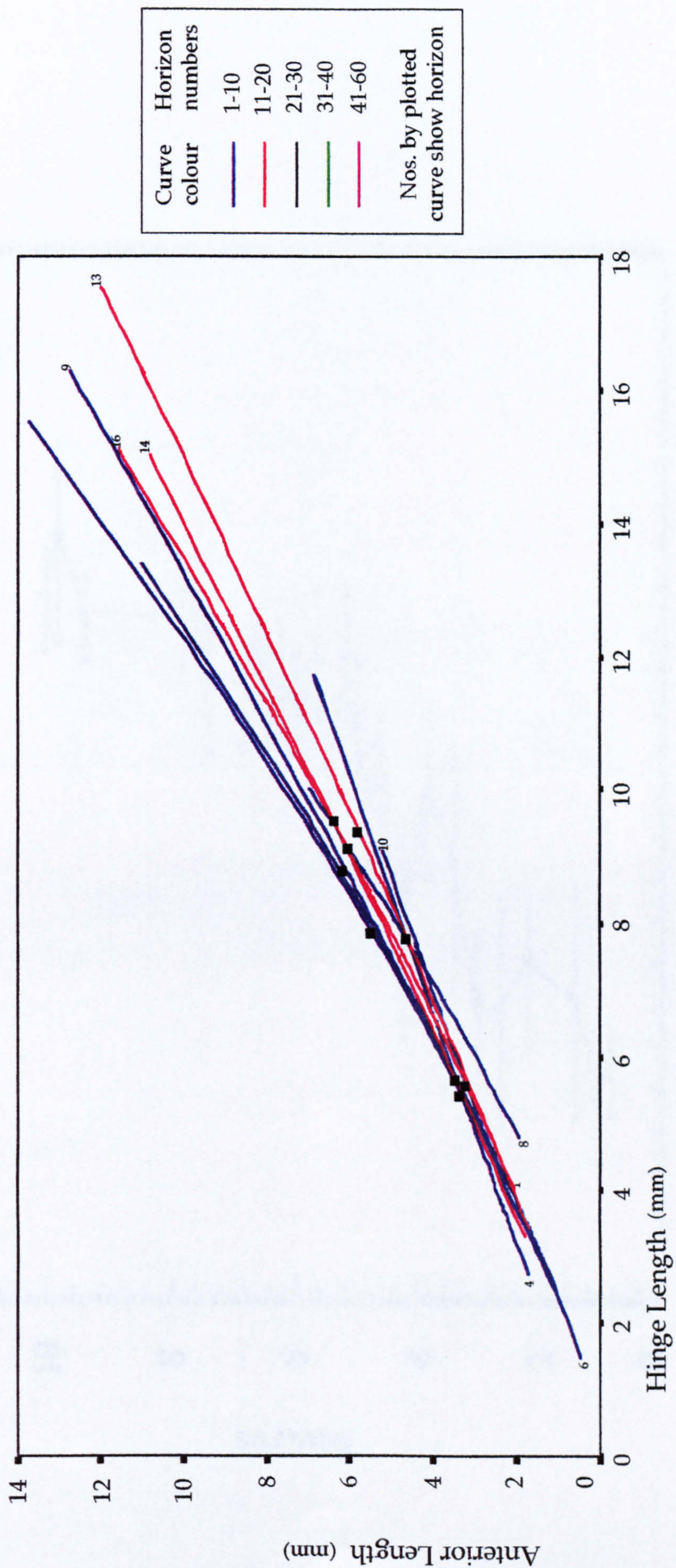


Figure 7.41. Growth curves for *M. braamburiensis*, Hinge Length against Anterior Length, Orton pit, with horizons n>13; sample means seen in Figure 7.38.



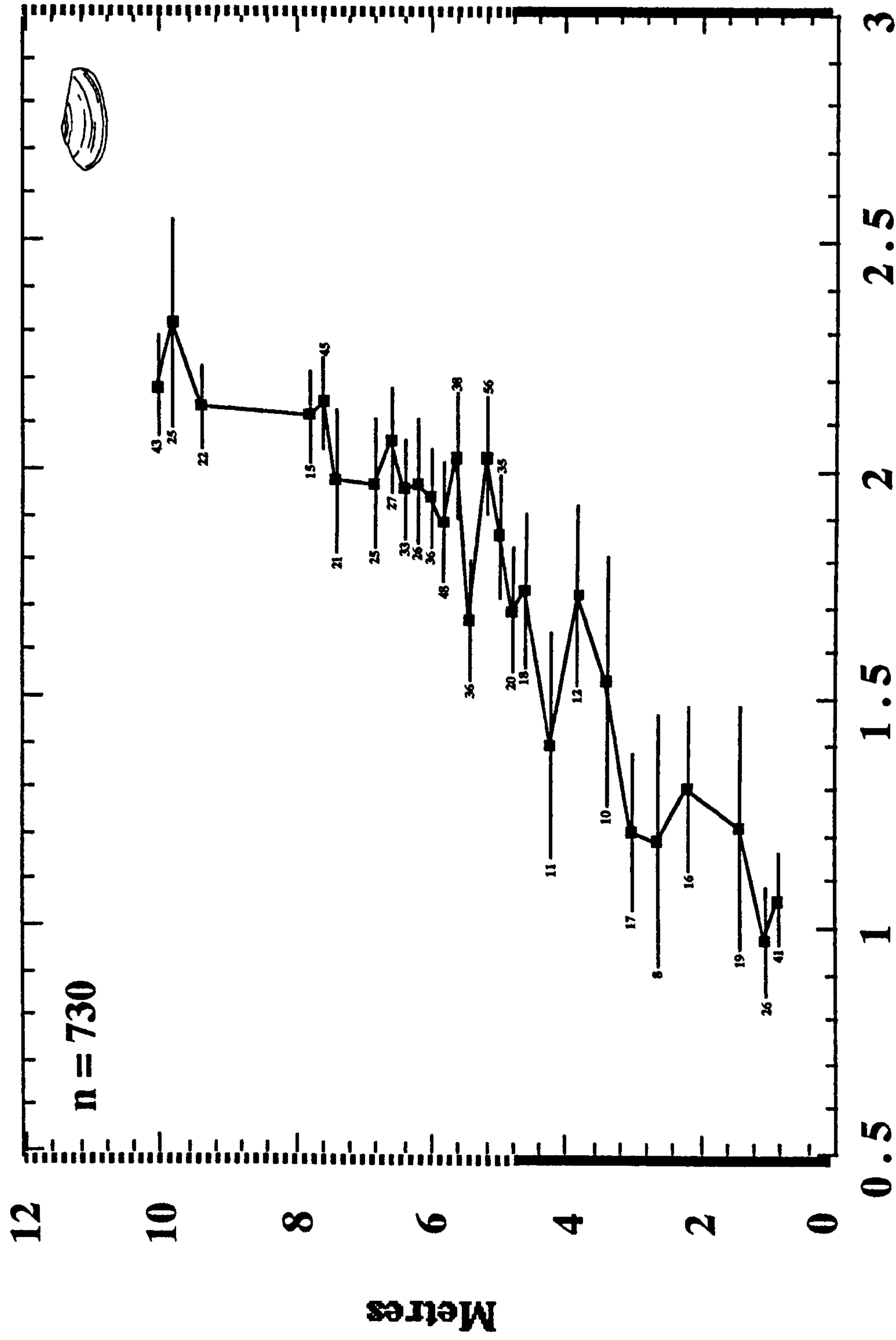


Figure 7.42. Hinge Length to Anterior Length ratio for *Mesosaccella morrisi*, Calvert pit. Error bars represent 95% confidence intervals. Sample sizes are total number of measured individuals for each sample mean.

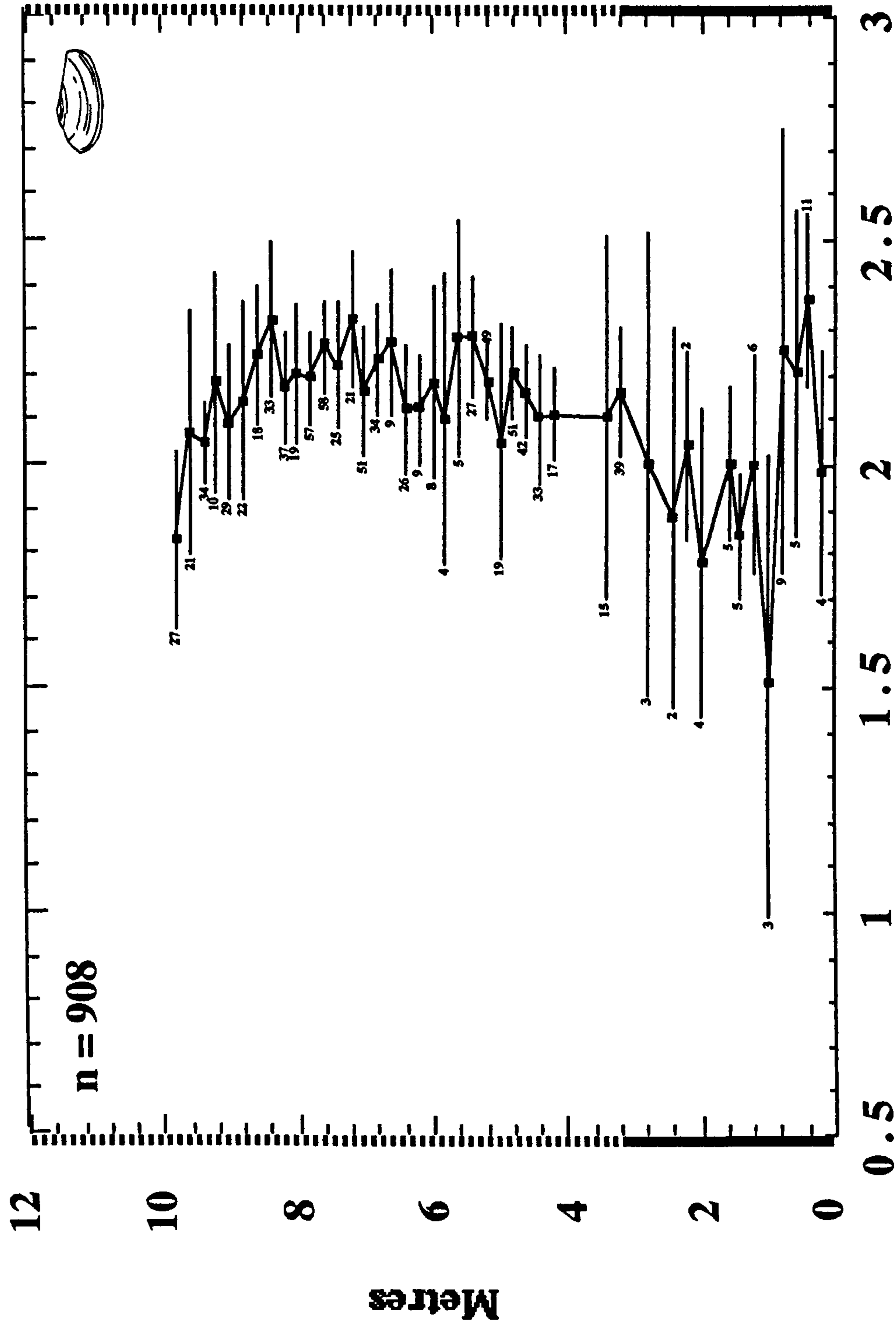


Figure 7.43. Hinge Length to Anterior Length ratio for *Mesosacella morrisi*, Saxon pit. Error bars represent 95% confidence intervals. Sample sizes are total number of measured individuals for each sample mean.

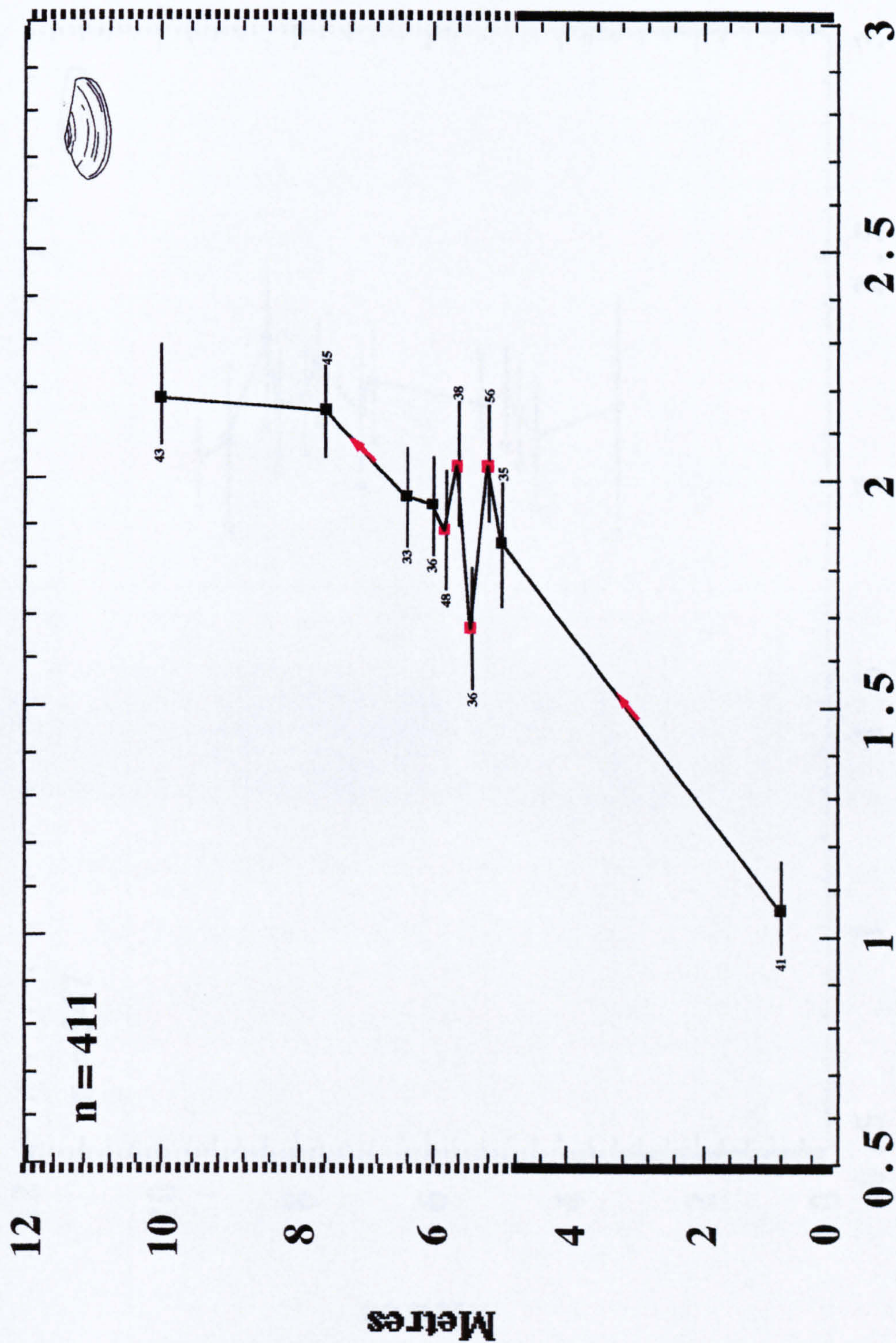


Figure 7.44. Hinge Length to Anterior Length ratio for *Mesosaccella morrissi*, Calvert pit. Error bars represent 95% confidence intervals. Each sample mean = $n > 27$. Black sample means = isometric growth; red sample means = allometric growth. (For all data see Figure 7.42).

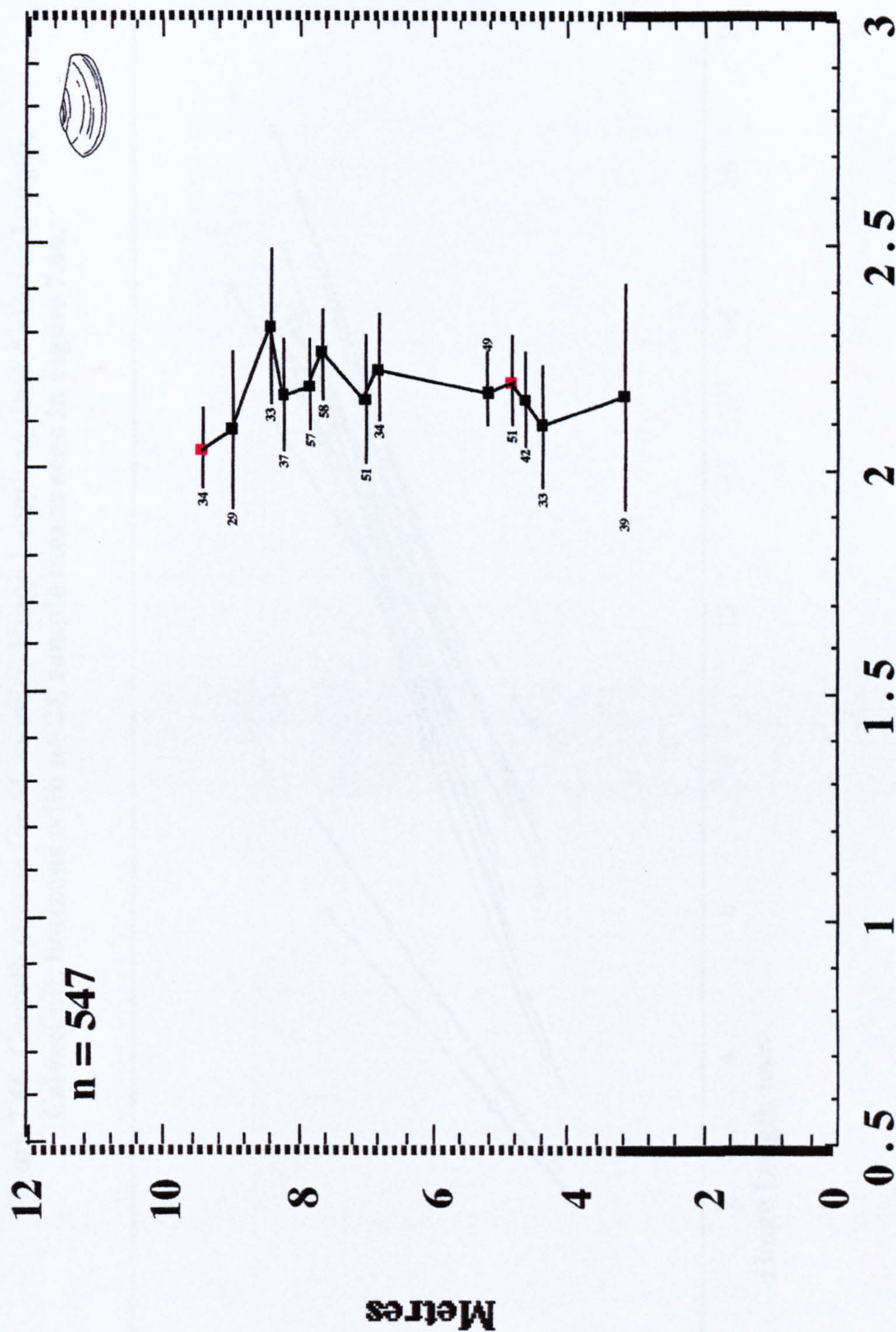


Figure 7.46. Growth curves for *M. morrisi*, Hinge Length against Anterior Length, Calvert pit, horizons with $n > 24$; sample means seen in Figure 7.44.

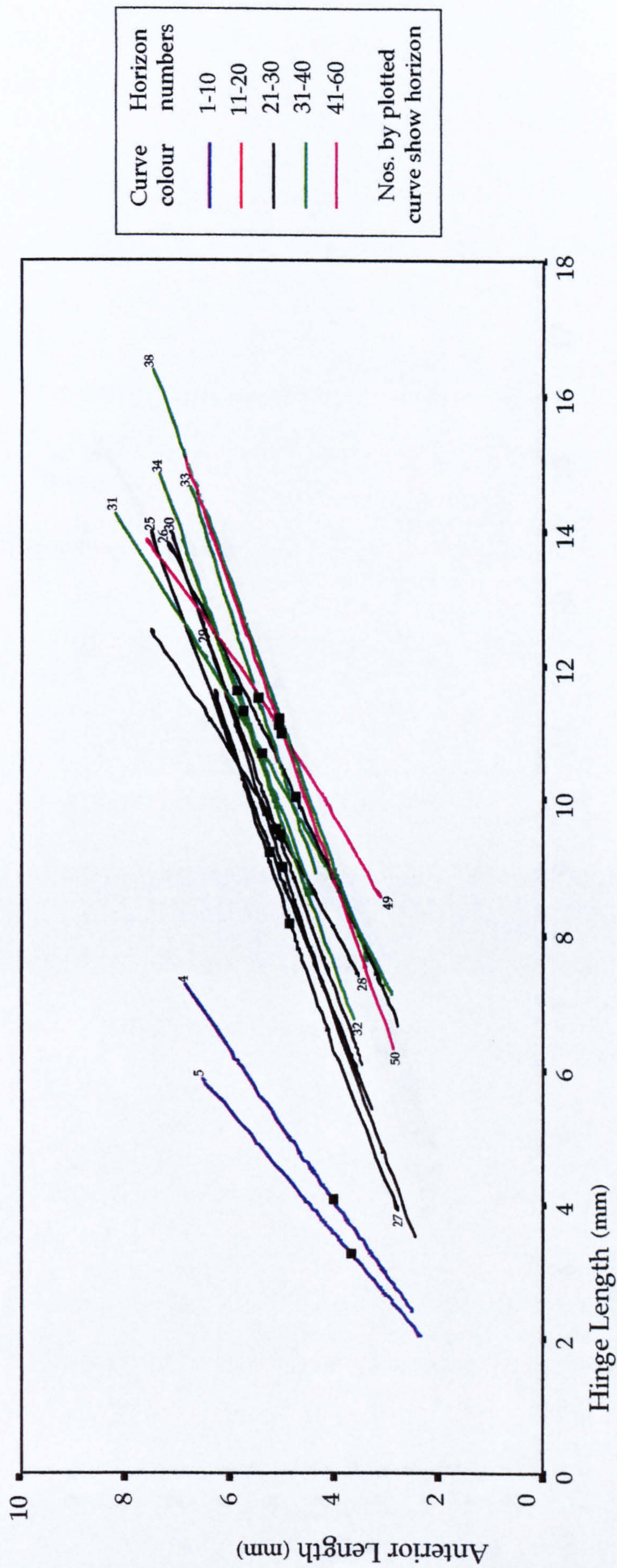
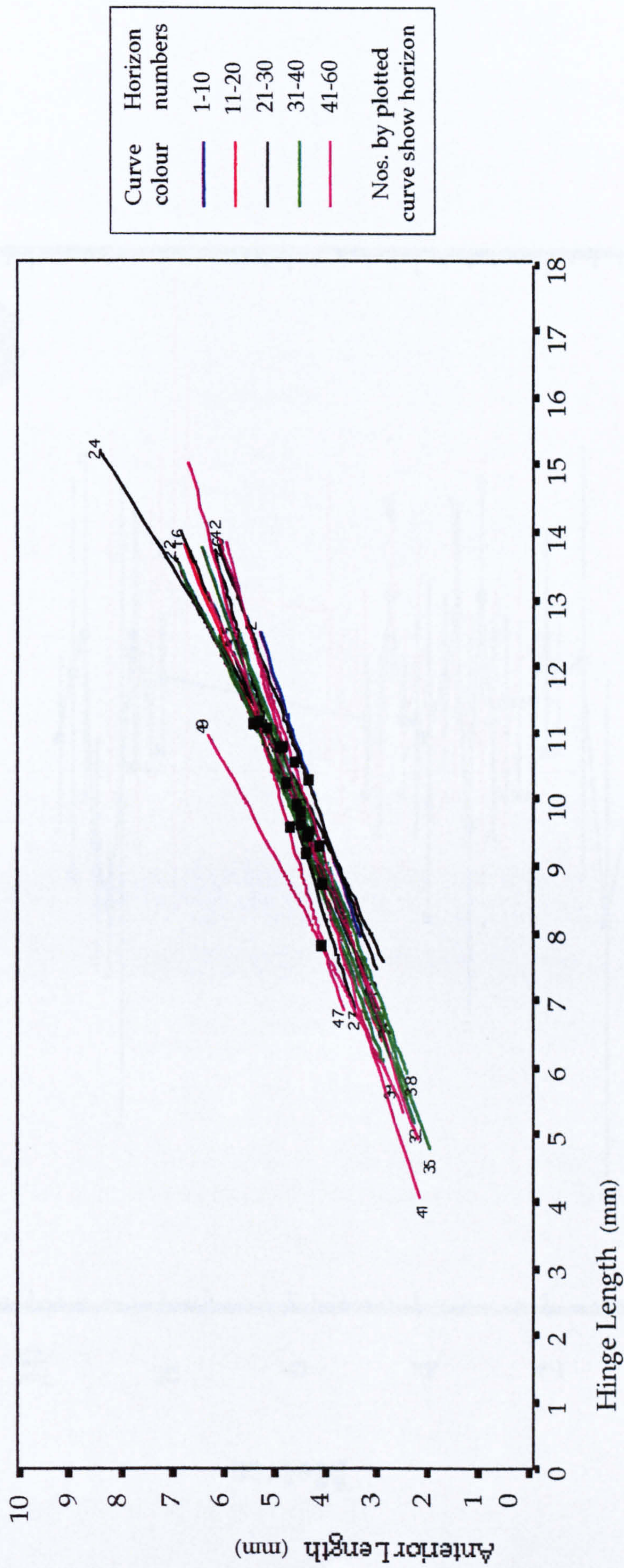


Figure 7.47. Growth curves for *M. morrisi*, Hinge Length against Anterior Length, Saxon pit, with horizons n>24; sample means seen in Figure 7.45.



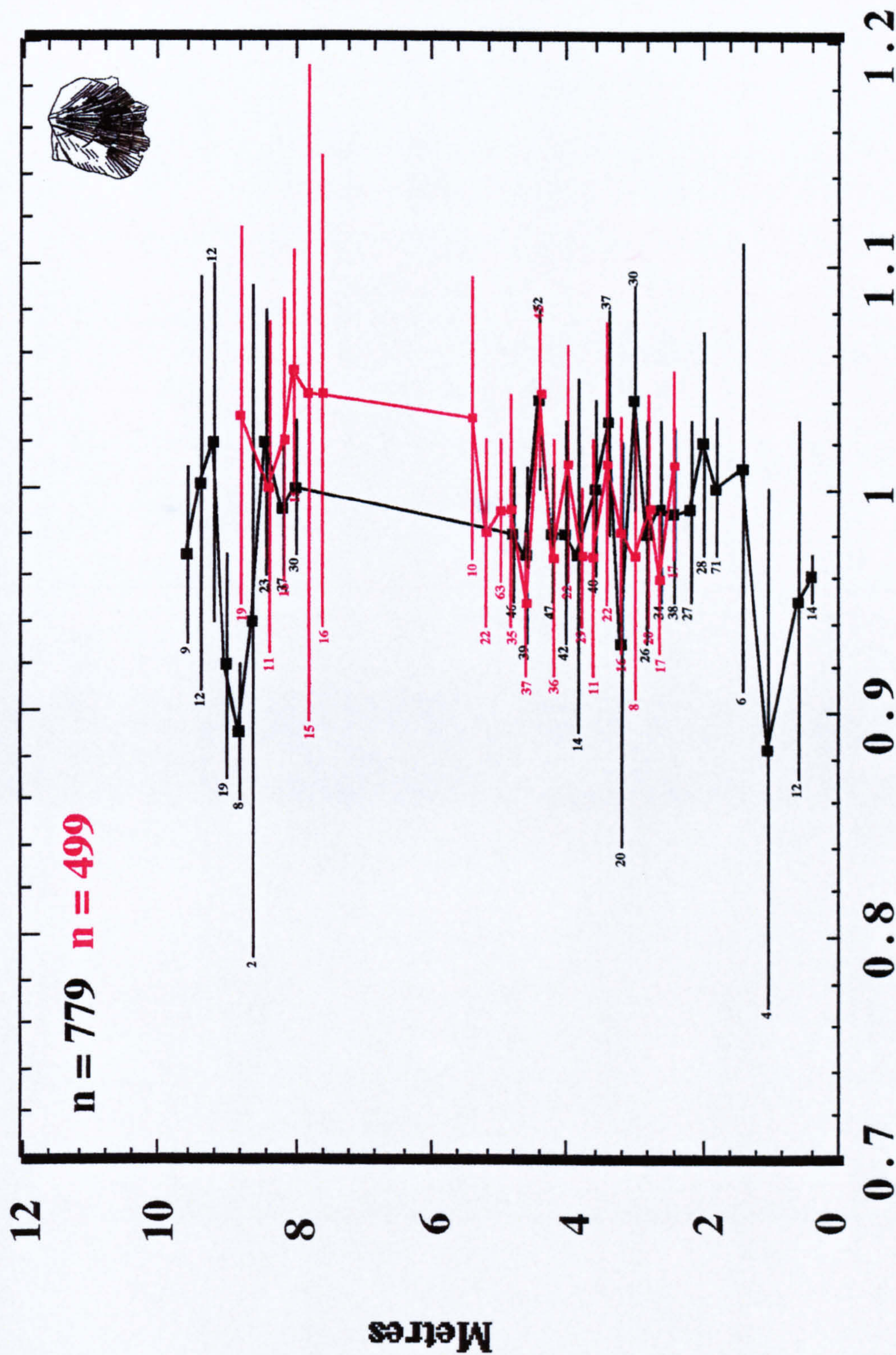


Figure 7.48. Length to Height ratio for *Meleagrionella braamburiensis*, Calvert pit in black, **Saxon pit in red** (data from Figures 7.18 & 7.19). Error bars represent 95% confidence intervals.

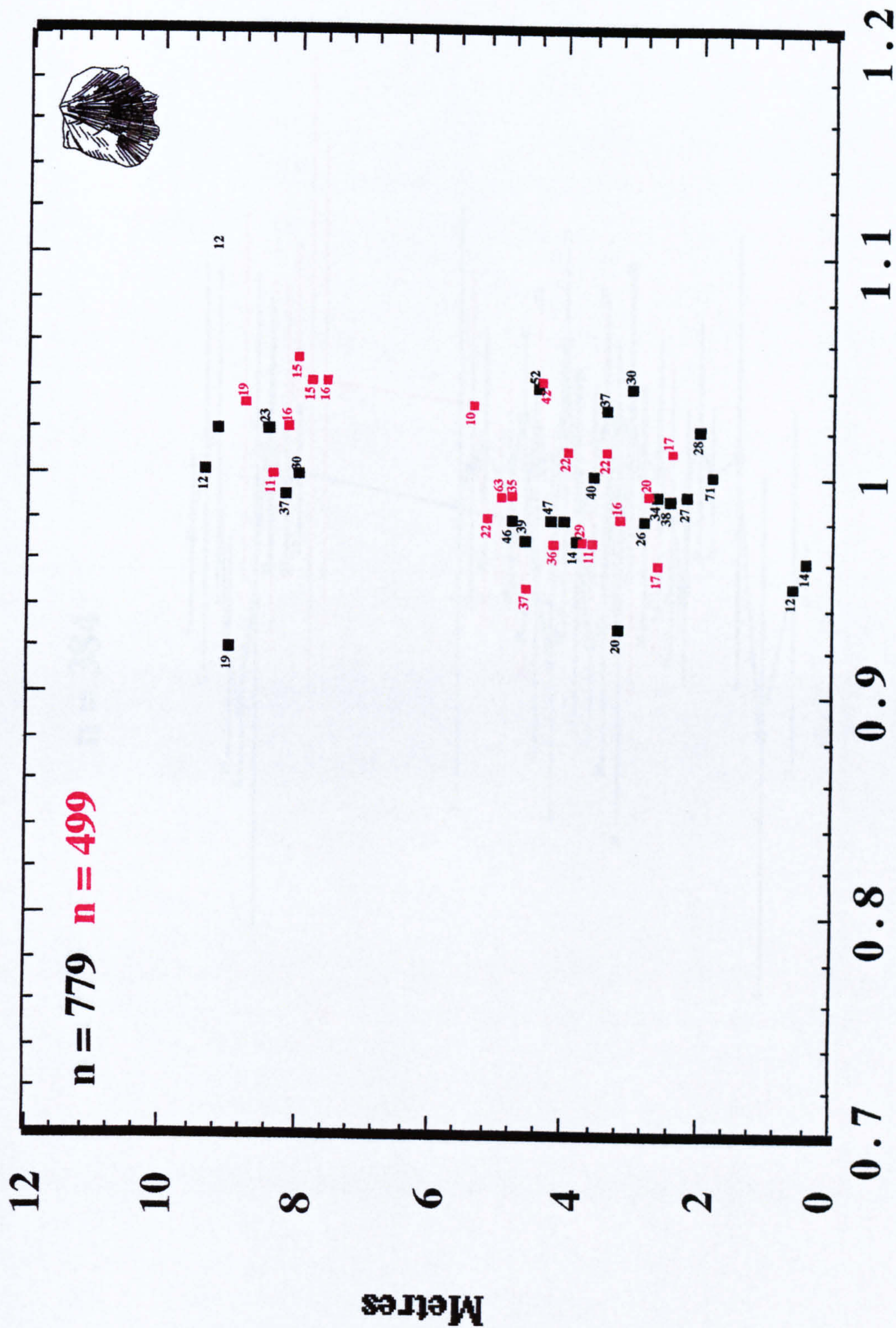


Figure 7.49. Length to Height ratio for *Meleagrionella braamburiensis*, Calvert pit in black, **Saxon pit in red**. Samples means = n>9 from Figures 7.18 & 7.19.

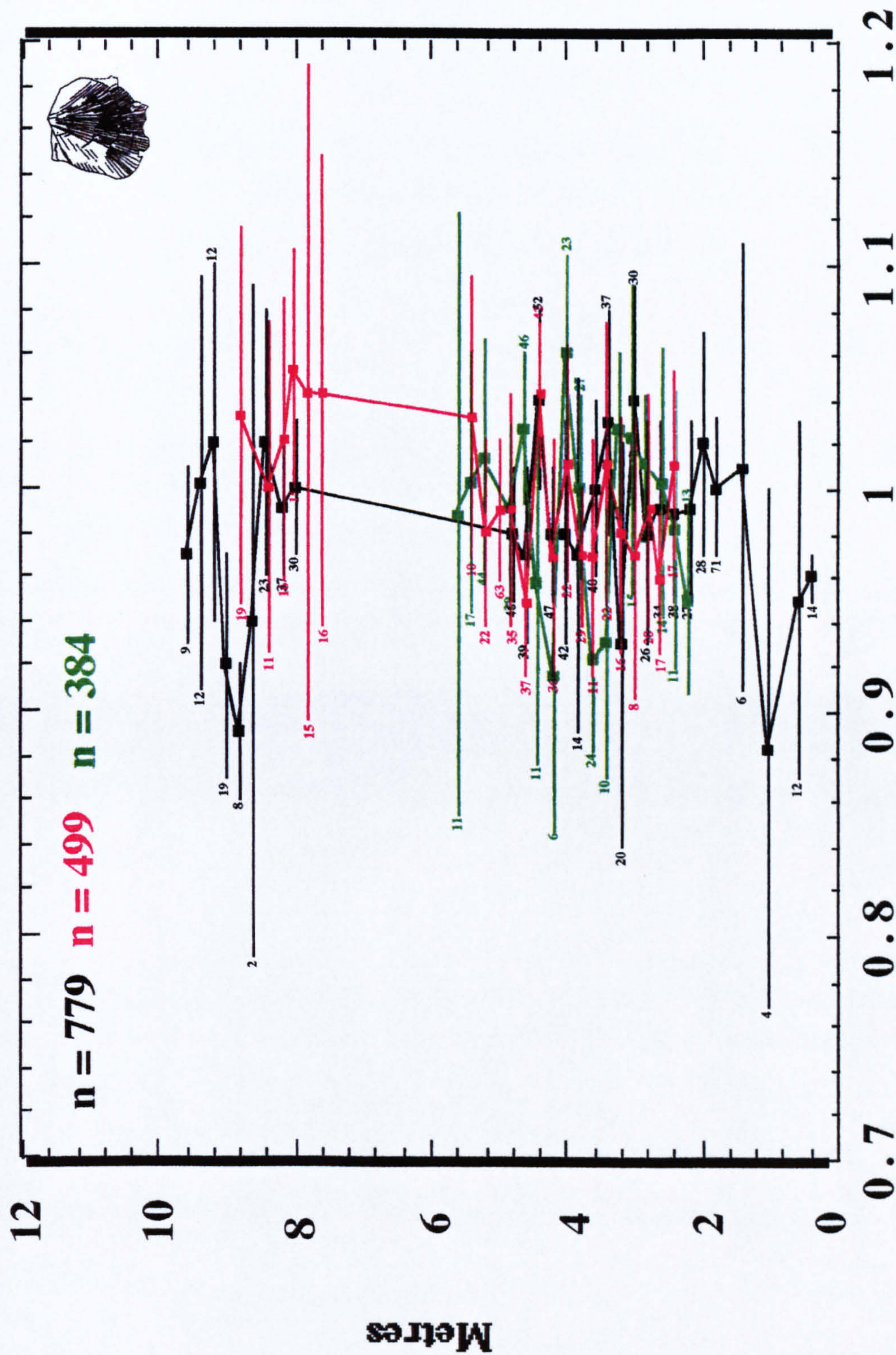
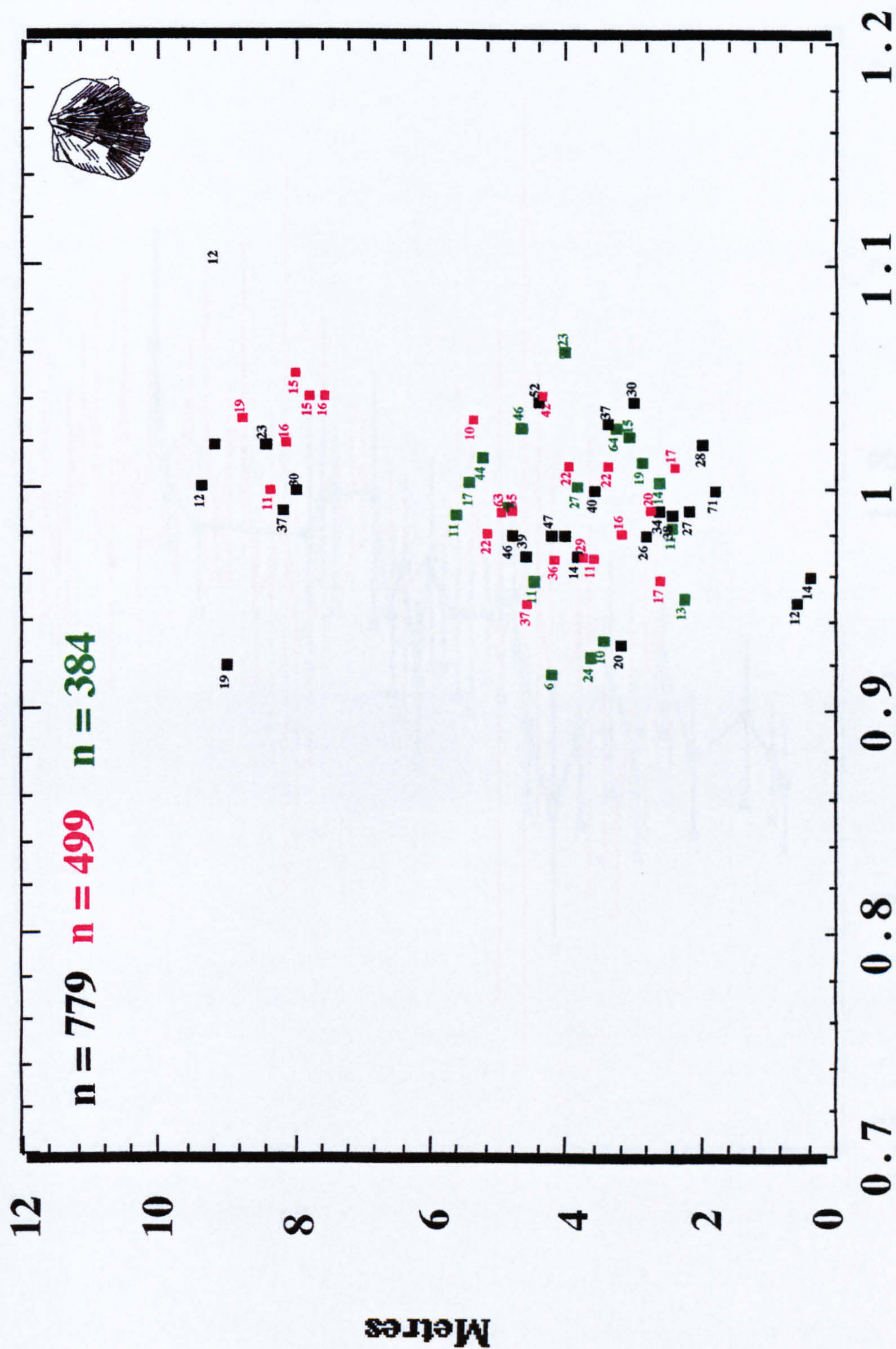


Figure 7.50. Length to Height ratio for *Meleagrinenella braamburiensis*, Calvert pit in black, Saxton pit in red, Orton pit in green (data from Figures 7.18, 7.19 & 7.20). Error bars represent 95% confidence intervals.



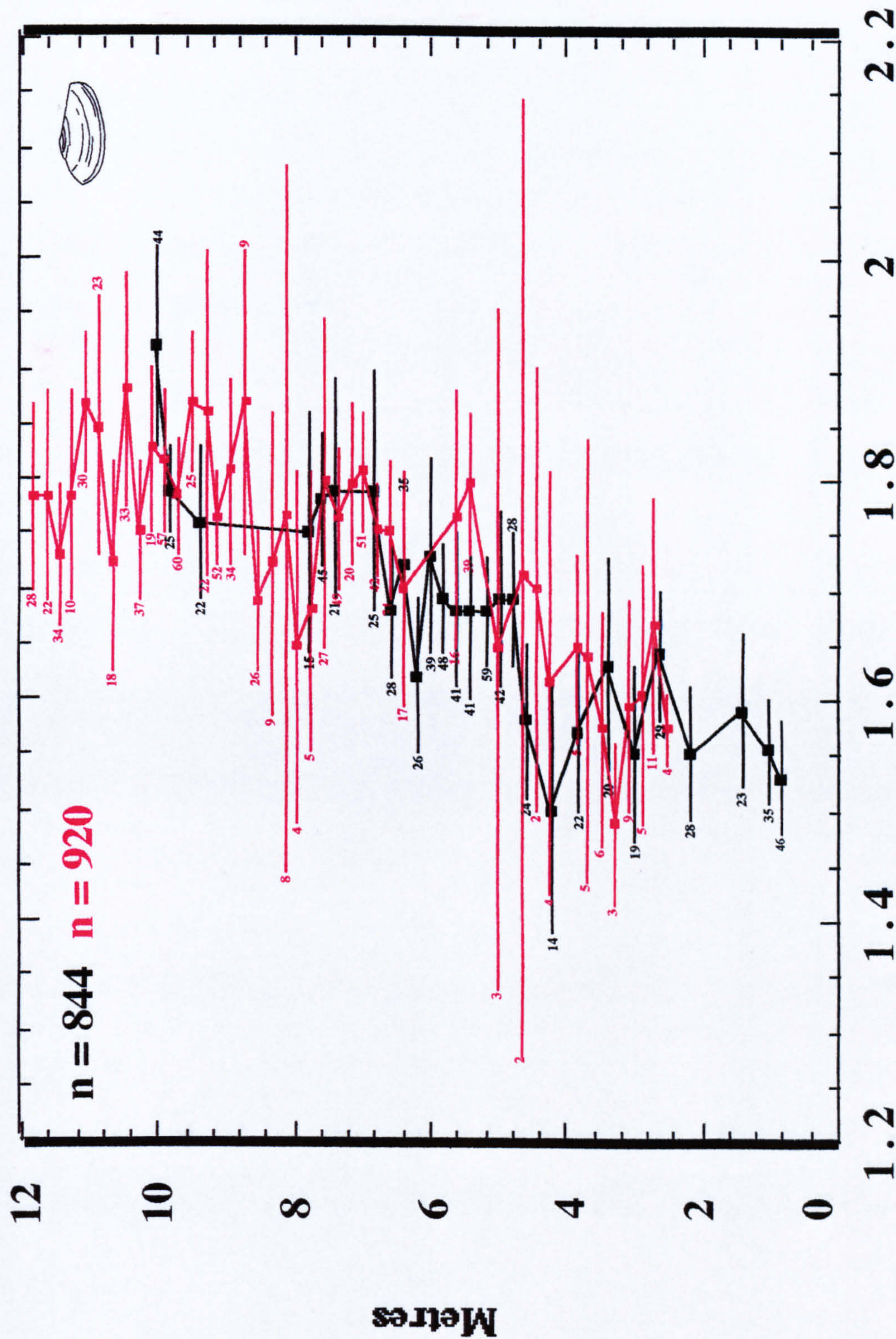


Figure 7.52. Length to Height ratio for *Mesosaccella morrisi*, Calvert pit in black, **Saxon pit in red** (data from Figures 7.27 & 7.28). Error bars represent 95% confidence intervals.

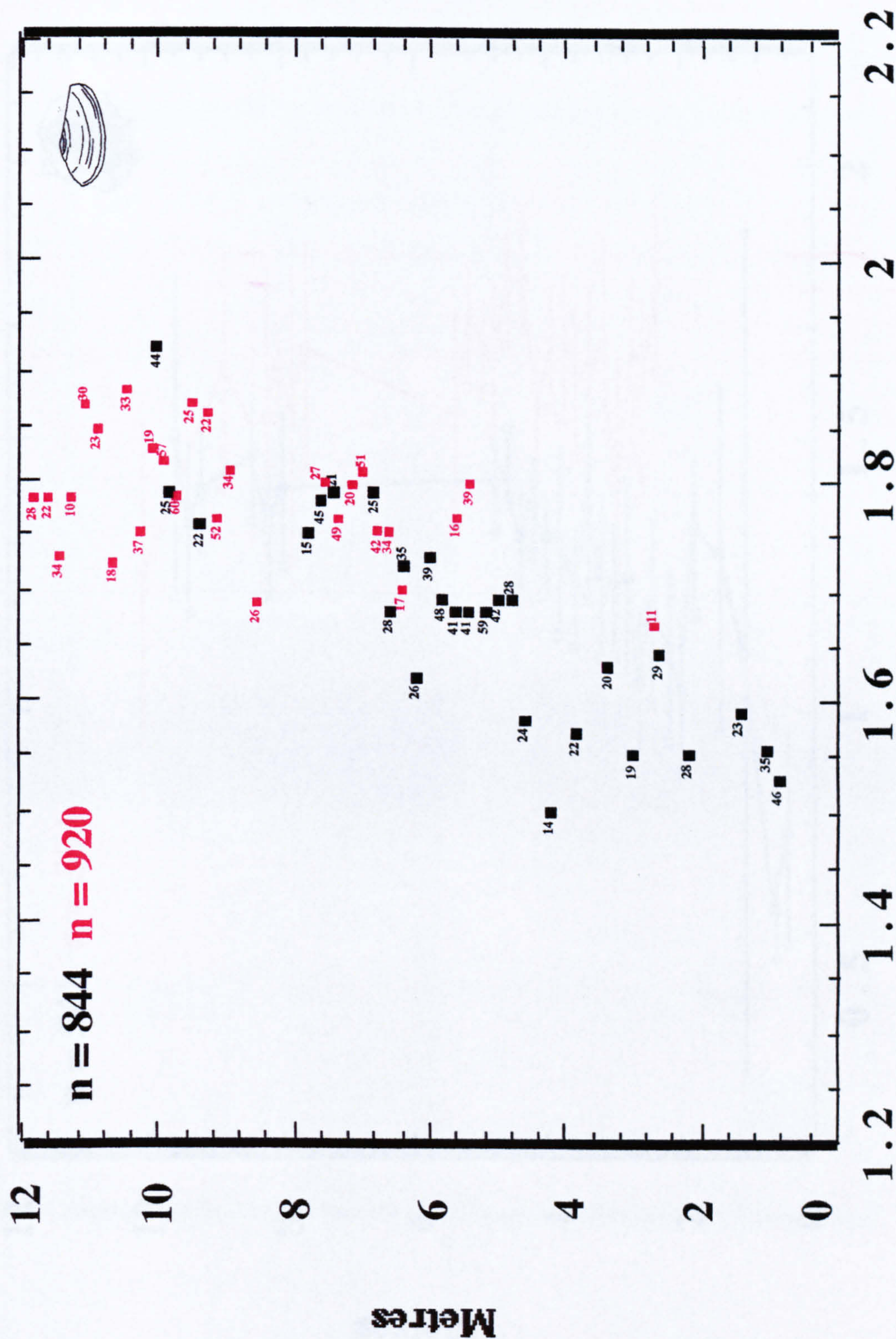


Figure 7.53. Length to Height ratio for *Mesosaccella morrisi*, Calvert pit in black, **Saxon pit in red**. Sample means = n>9 from Figures 7.27 & 7.28.

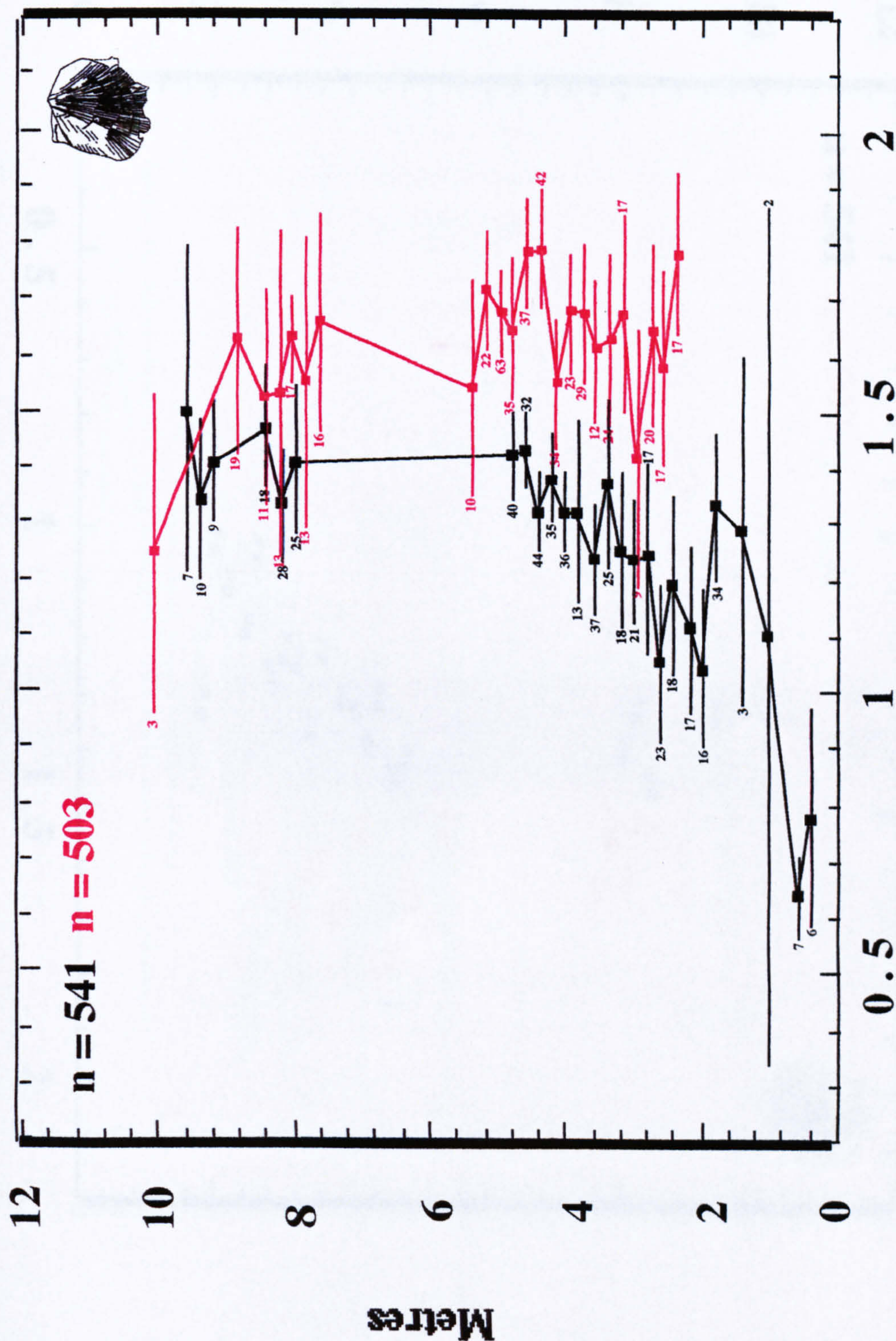


Figure 7.54. Hinge Length to Anterior Length ratio for *Meleagrionella braamburiensis*, Calvert pit in black, Saxon pit in red (data from Figures 7.33 & 7.34). Error bars represent 95% confidence intervals.

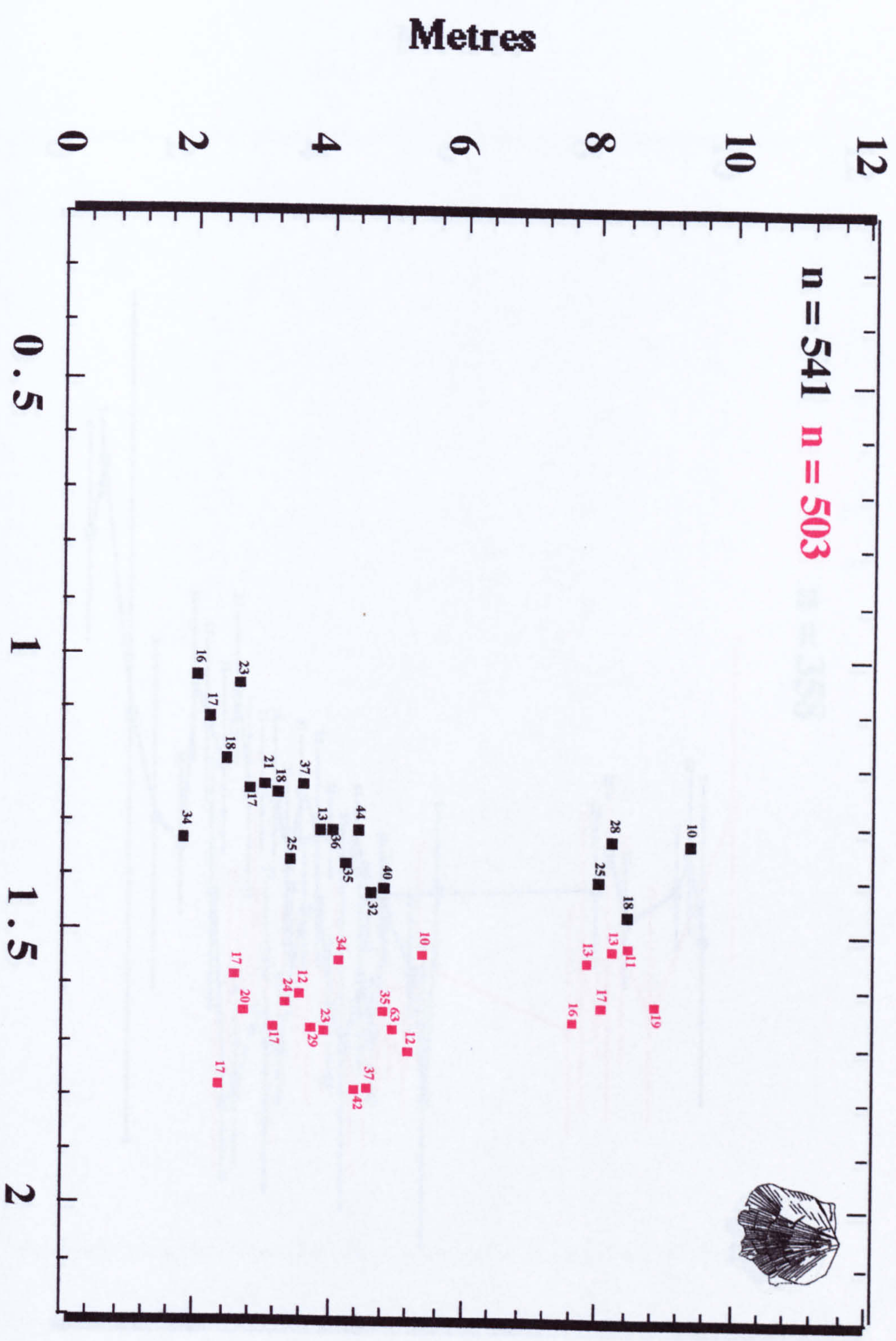


Figure 7.55. Hinge Length to Anterior Length ratio for *Melagrionella braamburienensis*, Calvert pit in black, Saxon pit in red. Sample means = $n > 9$ from Figures 7.33 & 7.34.

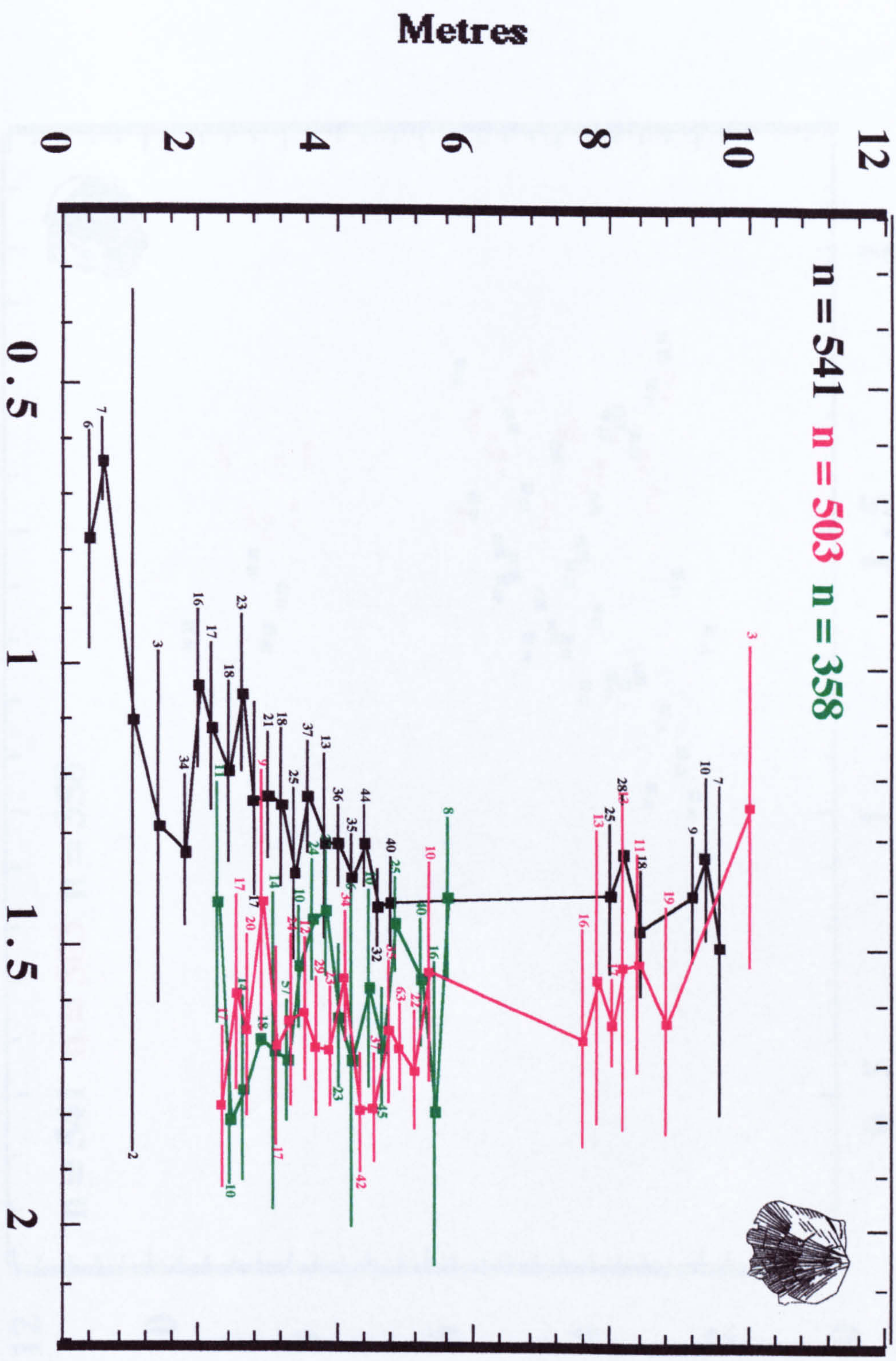


Figure 7.56. Hinge Length to Anterior Length ratio for *Melagrionella bramburriensis*, Calvert pit in black, Saxon pit in red, Orton pit in green (data from Figures 7.33, 7.34 & 7.35). Error bars represent 95% confidence intervals.

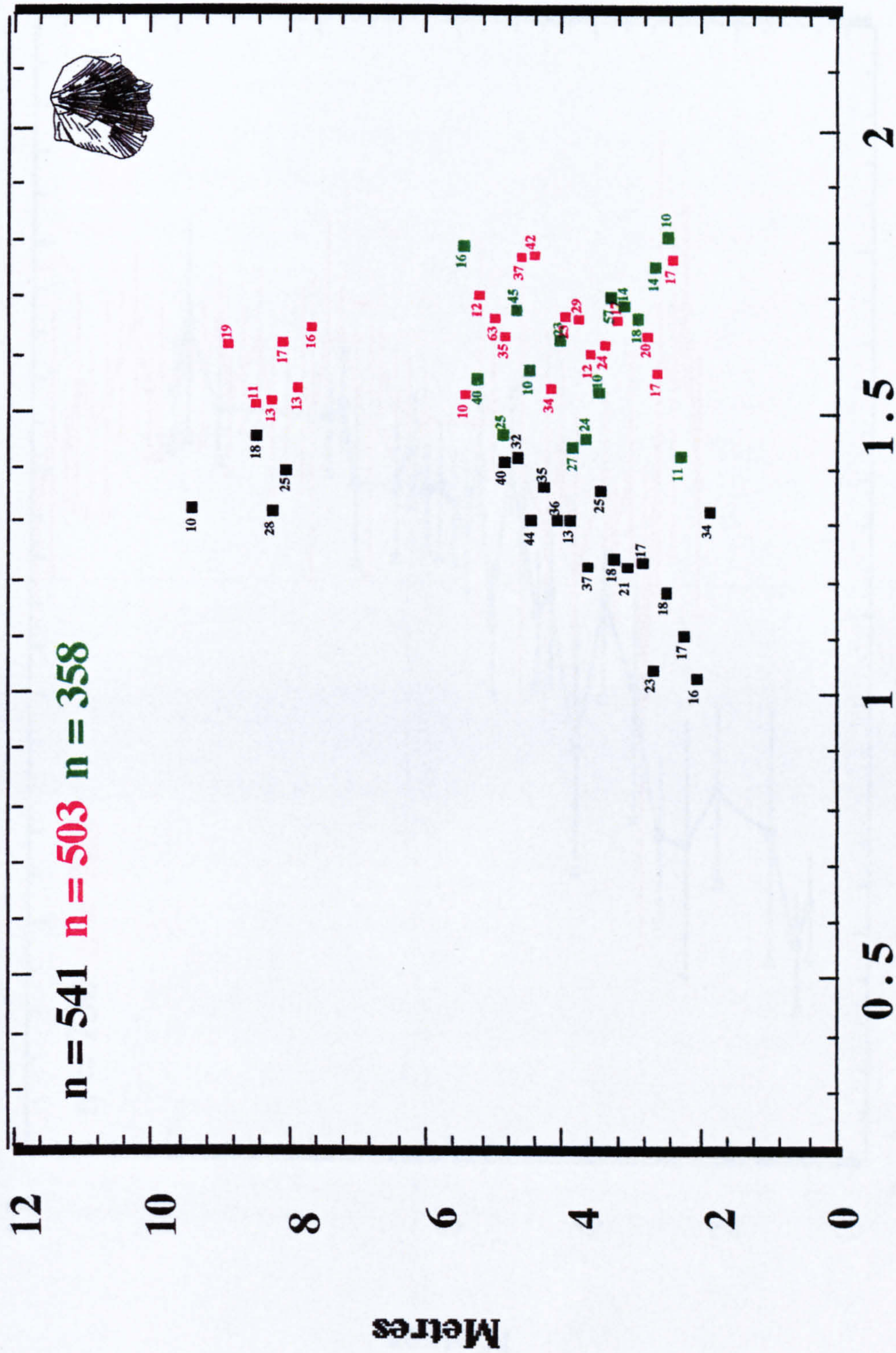


Figure 7.57. Hinge Length to Anterior Length ratio for *Meleagrinenella braamburiensis*,

Calvert pit in black, Saxon pit in red, Orton pit in green.

Sample means = $n > 9$ from Figures 7.33, 7.34 & 7.35.

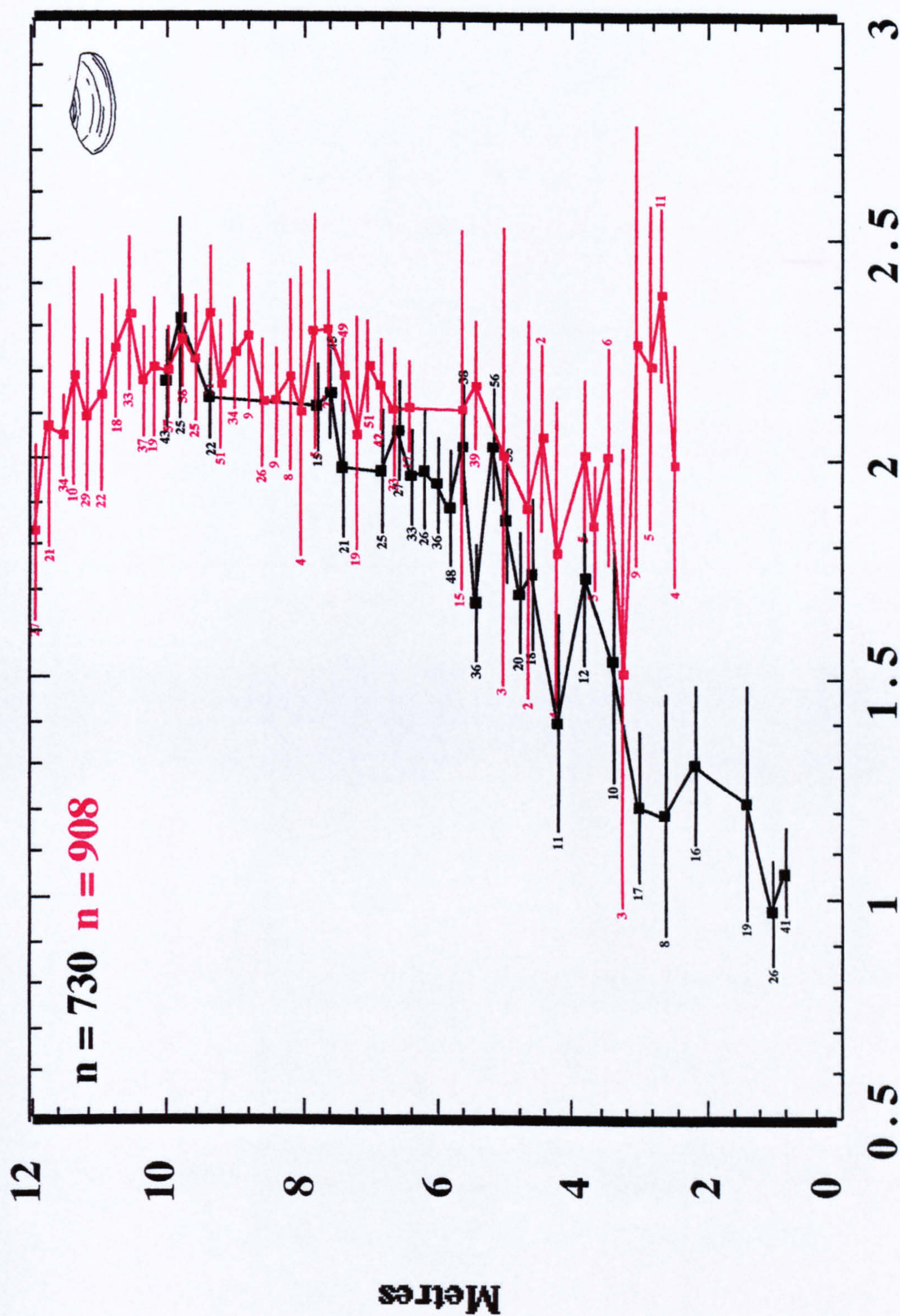


Figure 7.58. Hinge Length to Anterior Length ratio for *Mesosaccella morrisi*, Calvert pit in black, **Saxon pit in red** (data from Figures 7.42 & 7.43). Error bars represent 95% confidence intervals.

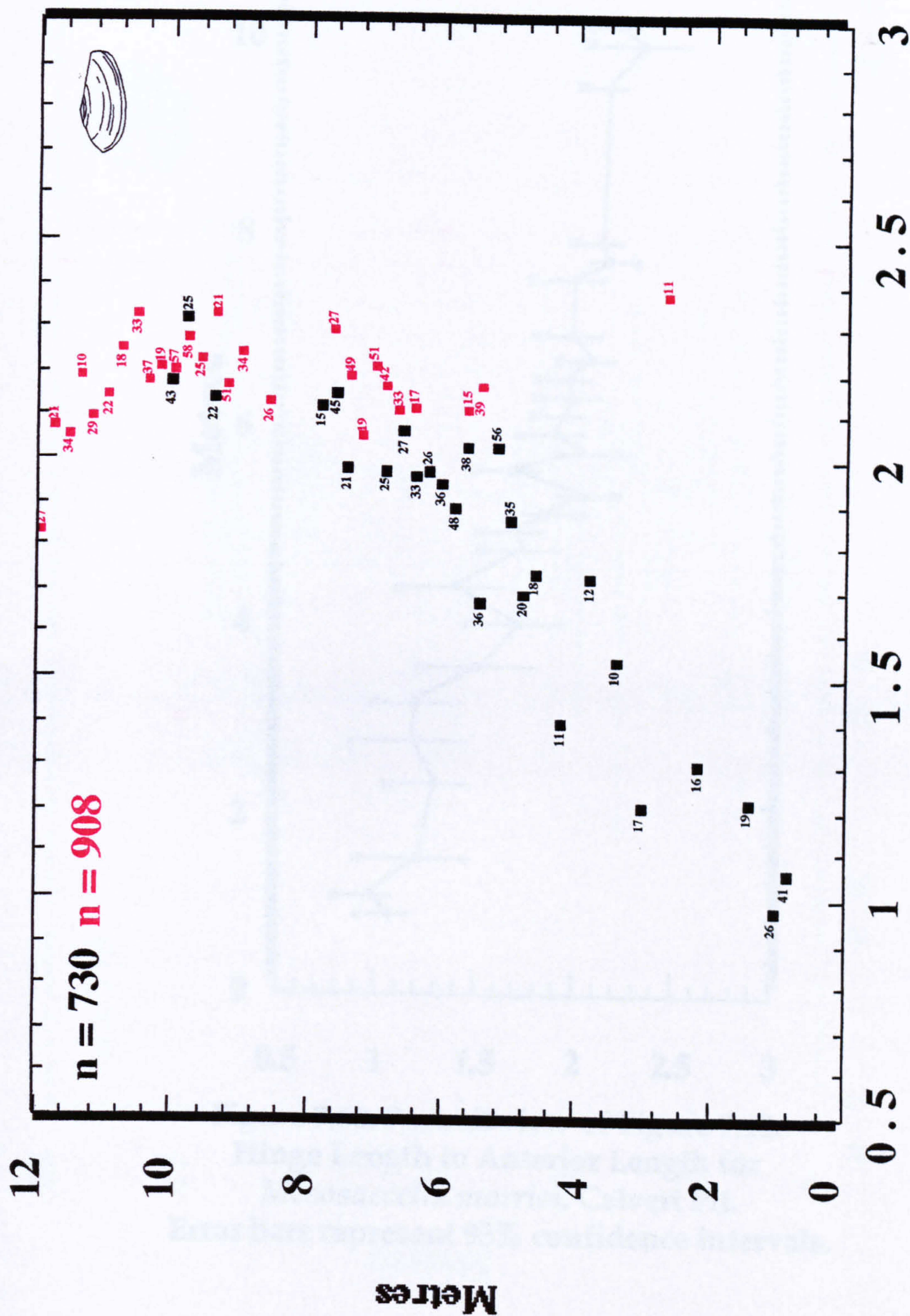


Figure 7.59. Hinge Length to Anterior Length ratio for *Mesosaccella morrisi*, Calvert pit in black, Saxon pit in red. Sample means = n>9 from Figures 7.42 & 7.43.

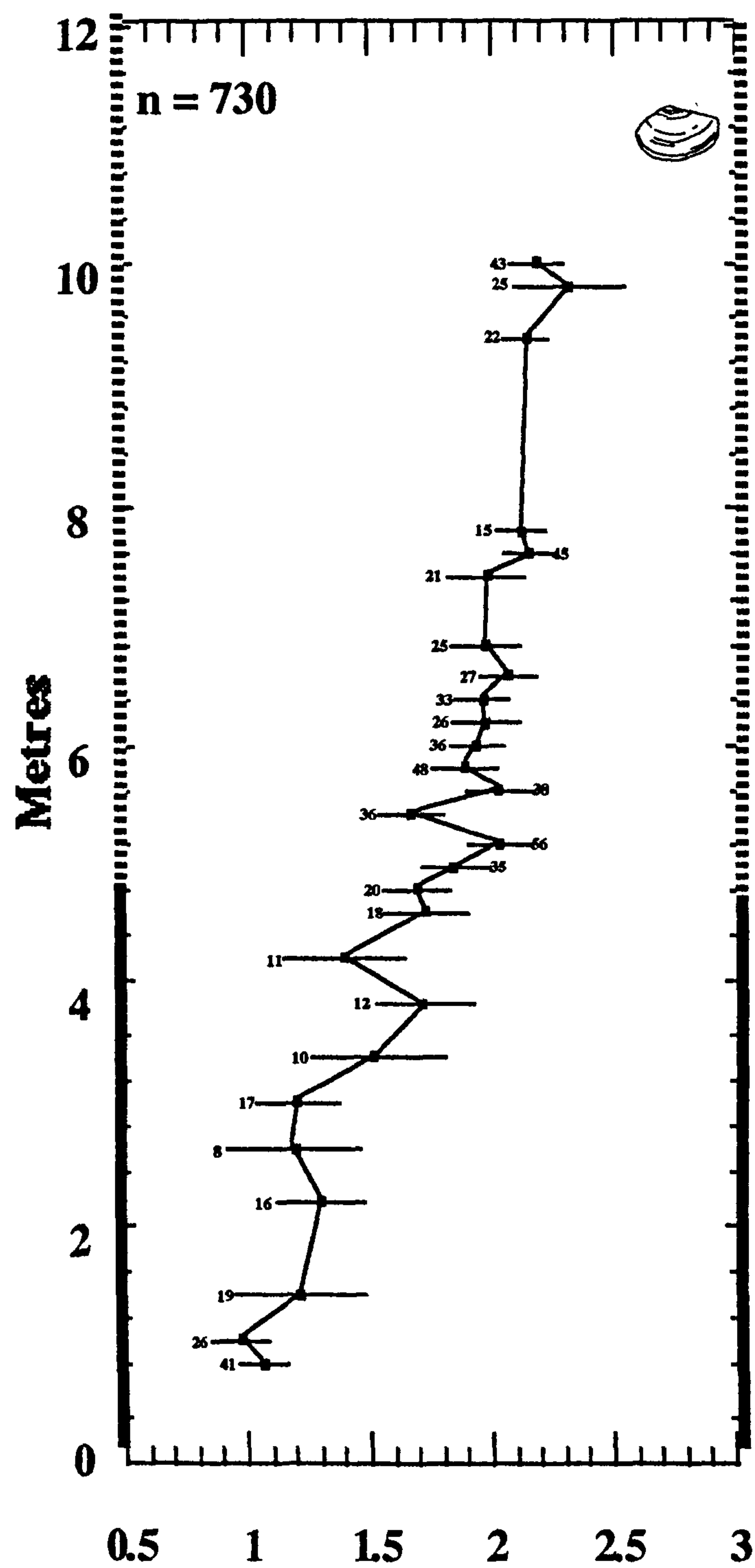


Figure 7.60. Portrait view of Figure 7.42:
Hinge Length to Anterior Length for
Mesosaccella morrisi, Calvert Pit.
Error bars represent 95% confidence intervals.

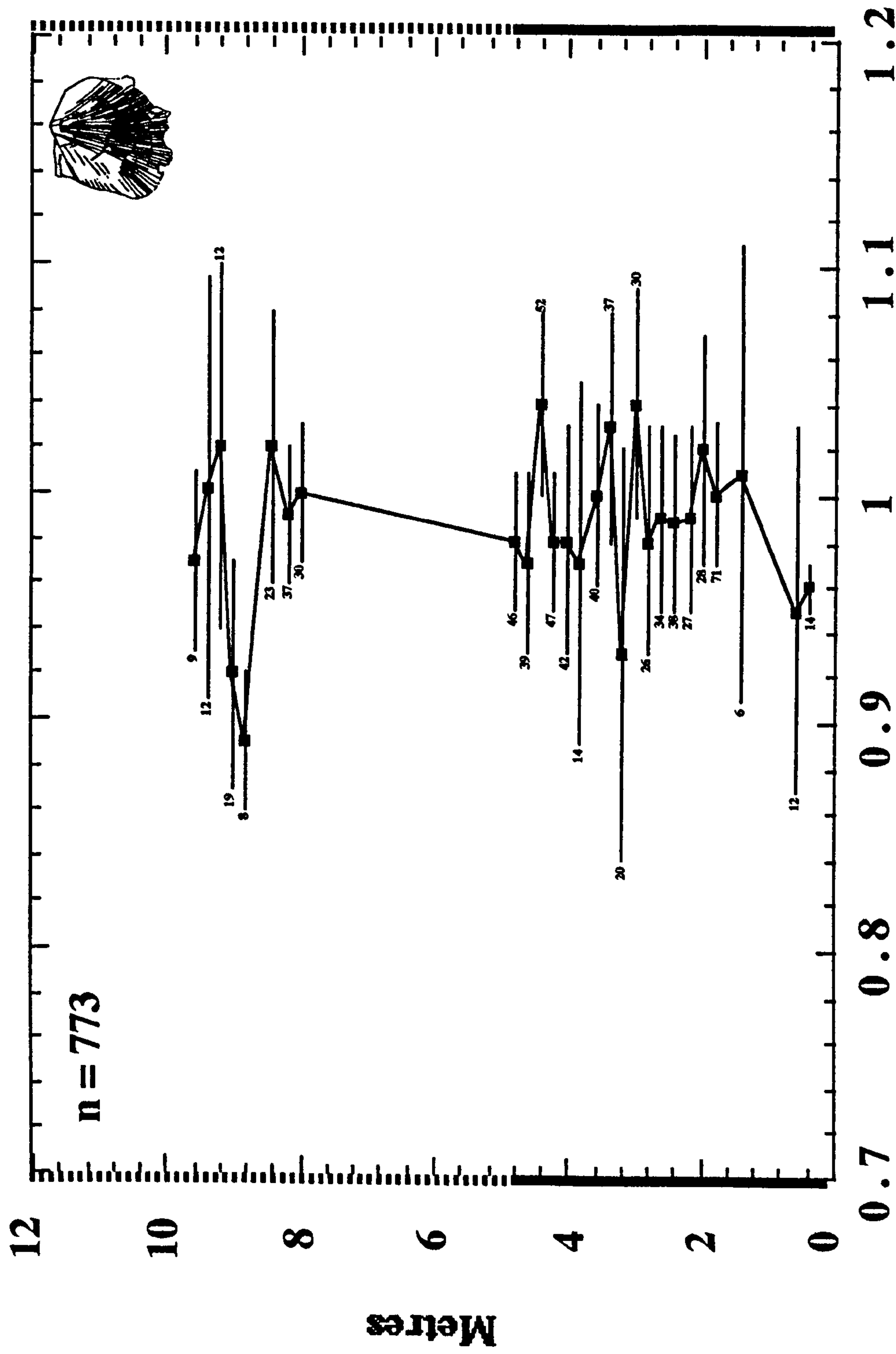


Figure 7.61. Length to Height ratio for *Meleagrionella braamburiensis*, Calvert pit, with sample means $n > 4$ (for all data see Figure 7.18). Error bars represent 95% confidence intervals.

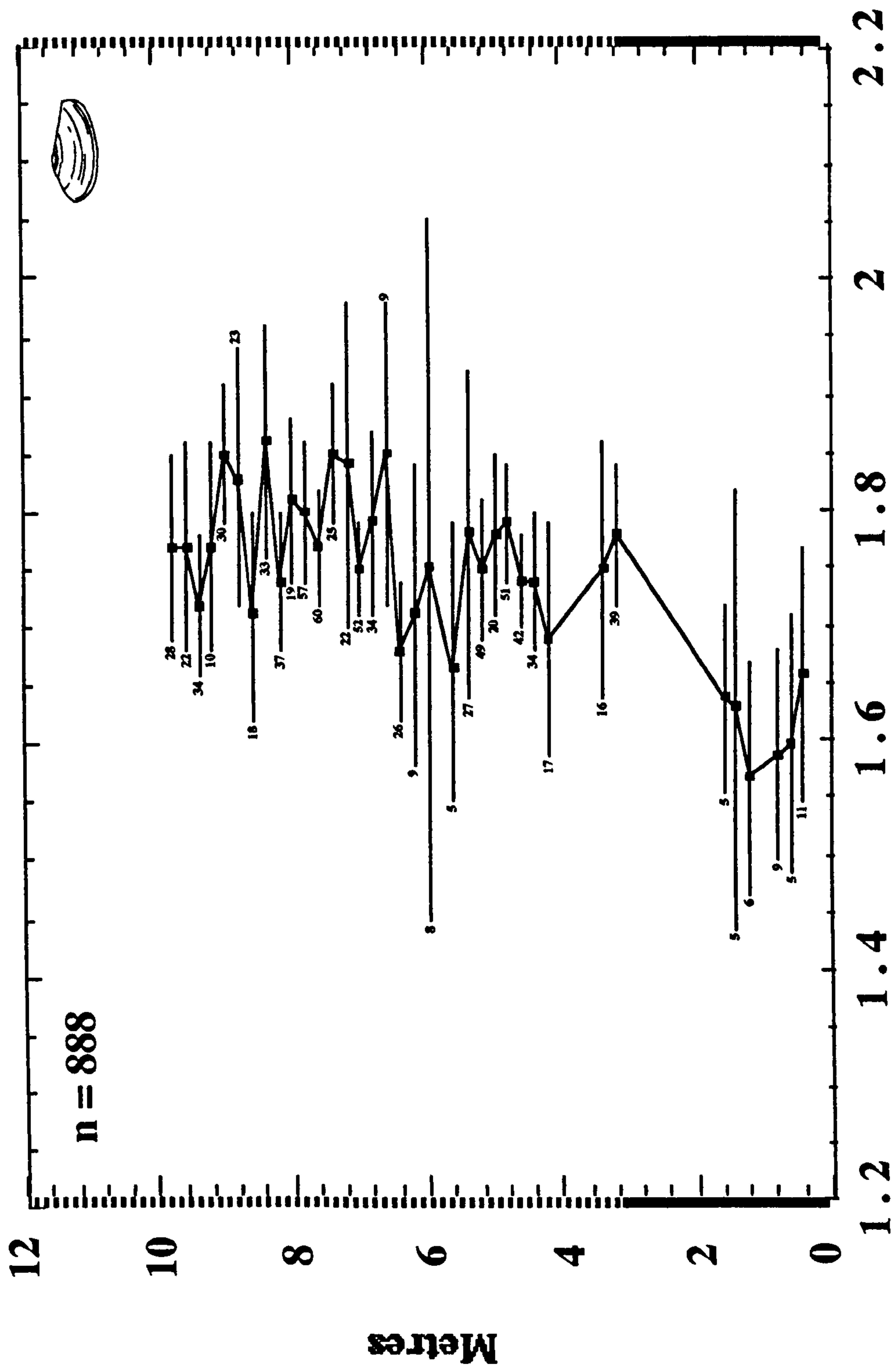


Figure 7.62. Length to Height ratio for *Mesosaccella morrisi*, Saxon pit, with sample means $n > 4$ (for all data see Figure 7.28). Error bars represent 95% confidence intervals.

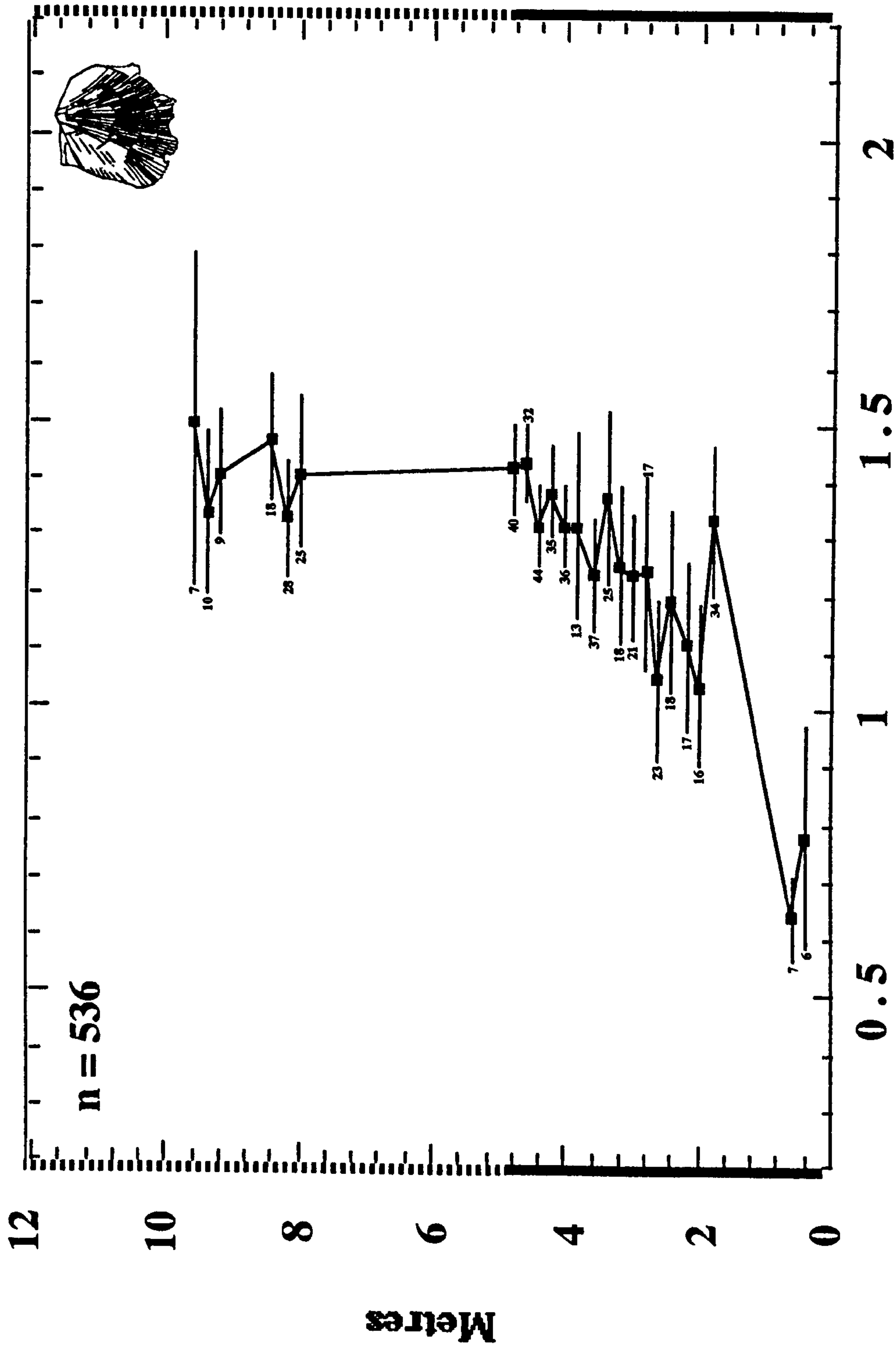


Figure 7.63. Hinge Length to Anterior Length ratio for *Meleagrinerella braamburiensis*, Calvert pit, with sample means $n > 4$ (for all data see Figure 7.33). Error bars represent 95% confidence intervals.

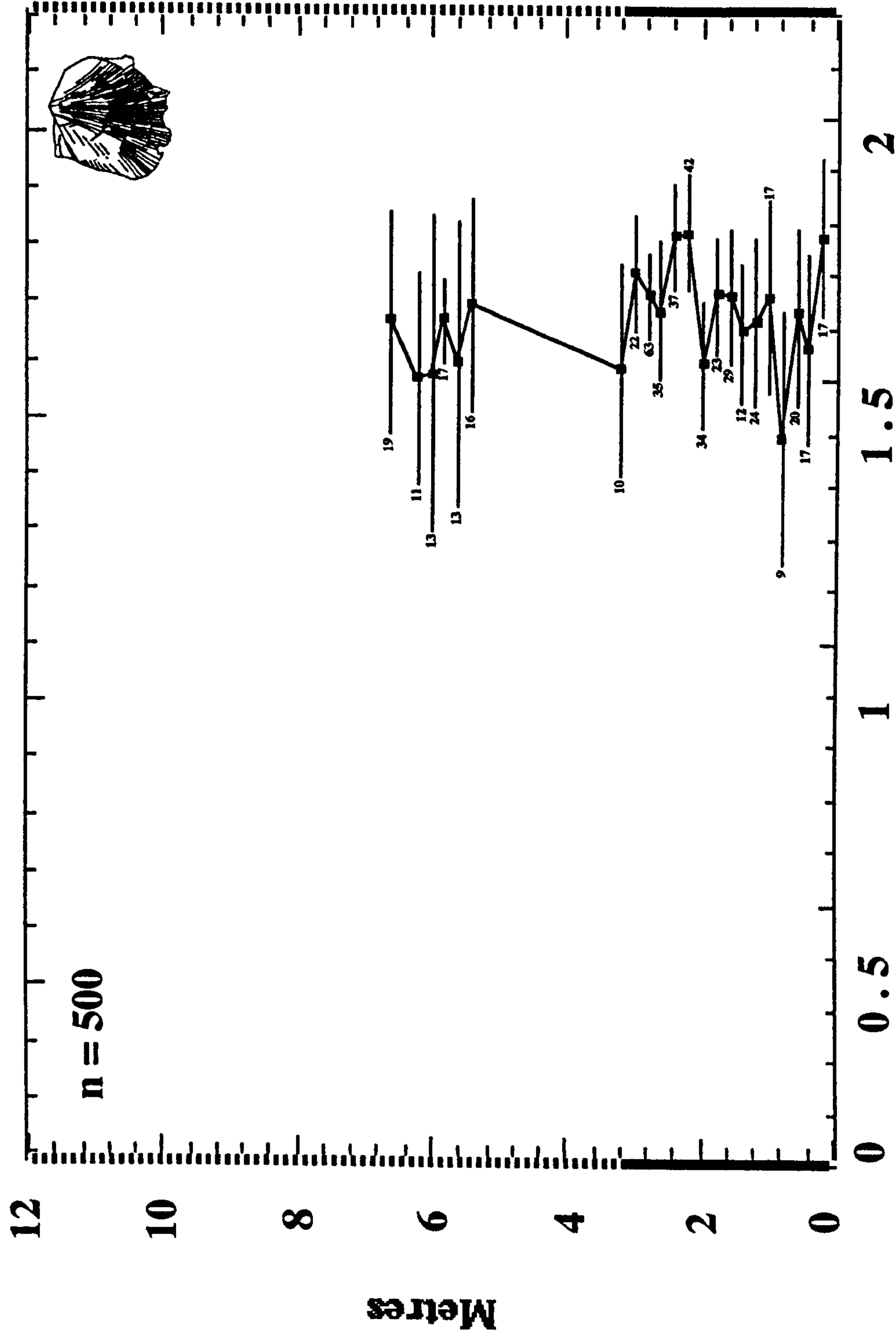


Figure 7.64. Hinge Length to Anterior Length ratio for *Meleagrinella braamburiensis*, Saxon pit, with sample means $n > 4$ (for all data see Figure 7.34). Error bars represent 95% confidence intervals.

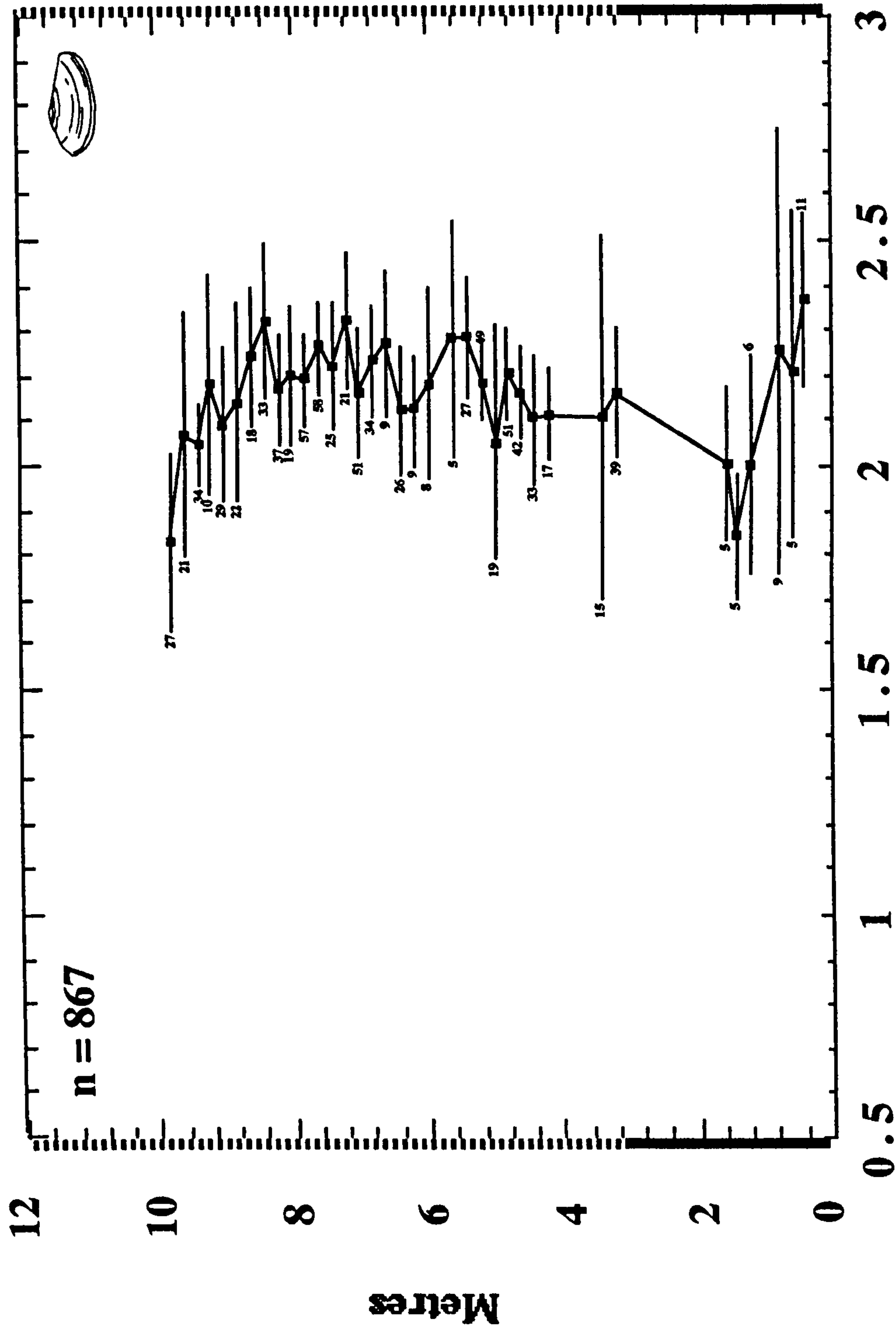


Figure 7.65. Hinge Length to Anterior Length ratio for *Mesosaccella morrisi*, Saxon pit, with sample means $n > 4$ (for all data see Figure 7.43). Error bars represent 95% confidence intervals.

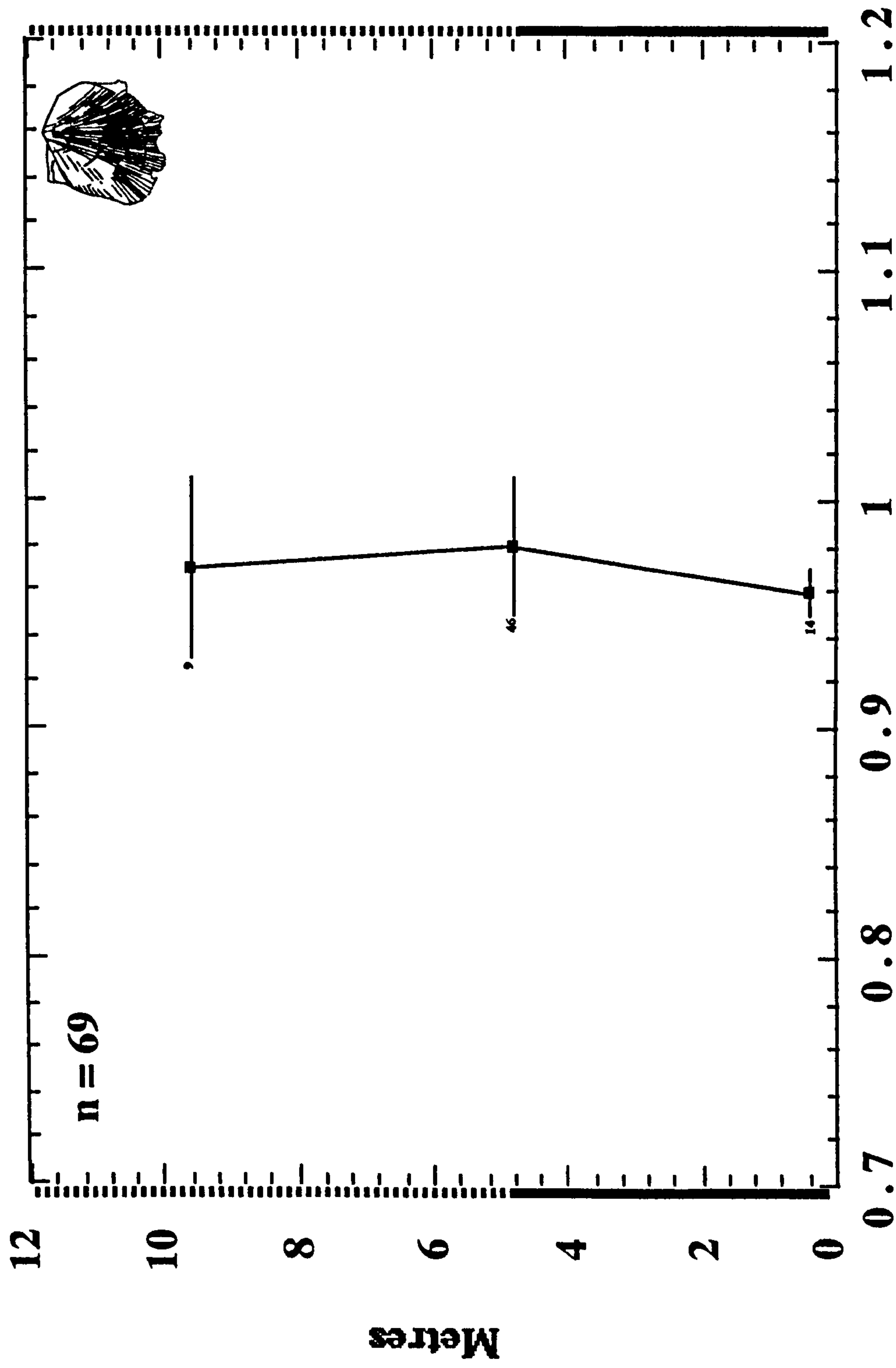


Figure 7.66. 3 individual sample means from the Length to Height ratio for *Meleagrinella braamburiensis*, Calvert pit (Figure 7.18).

Error bars represent 95% confidence intervals.

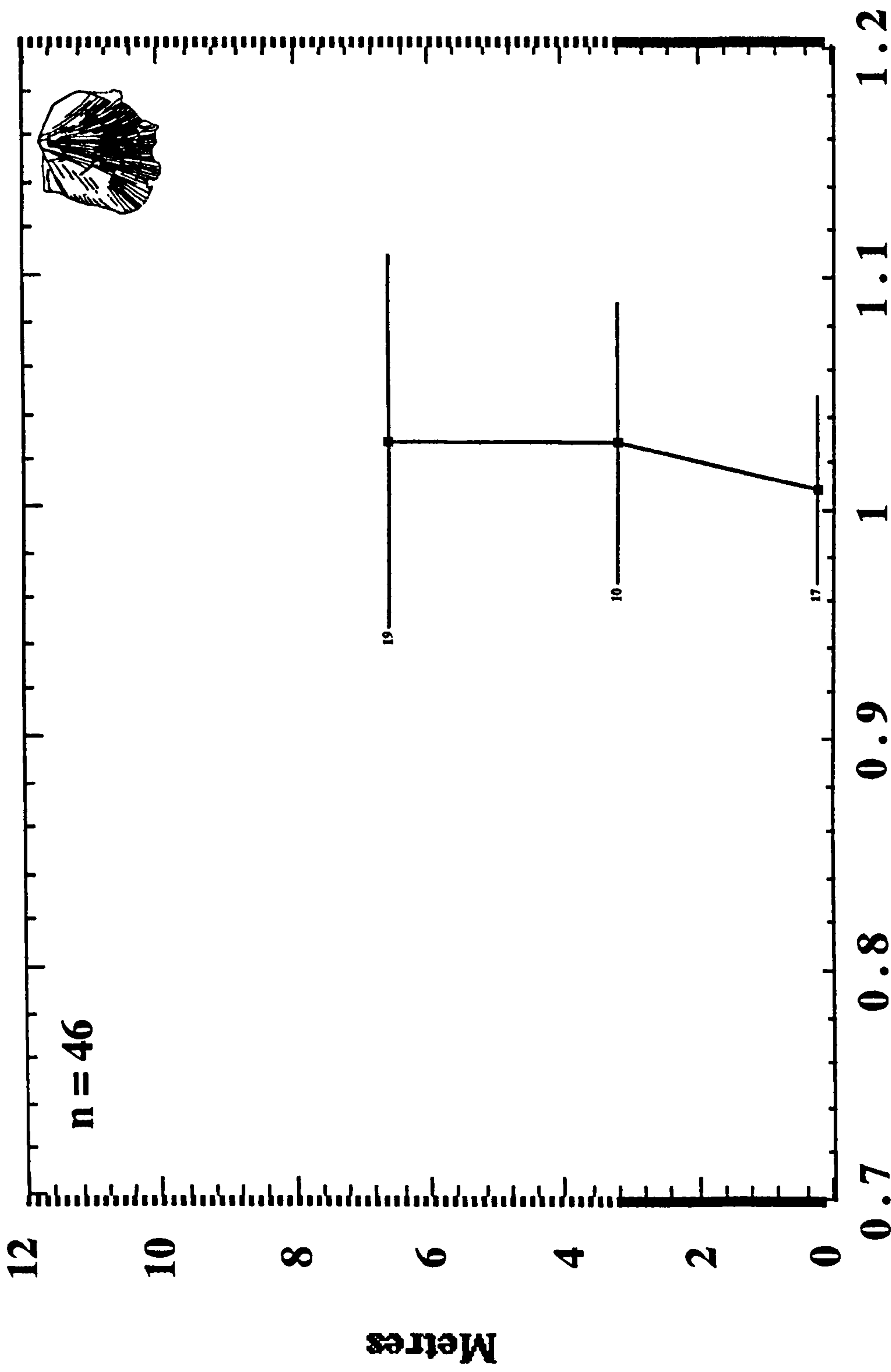


Figure 7.67. 3 individual sample means from the Length to Height ratio for *Meleagrinenella braamburiensis*, Saxon pit (Figure 7.19). Error bars represent 95% confidence intervals.

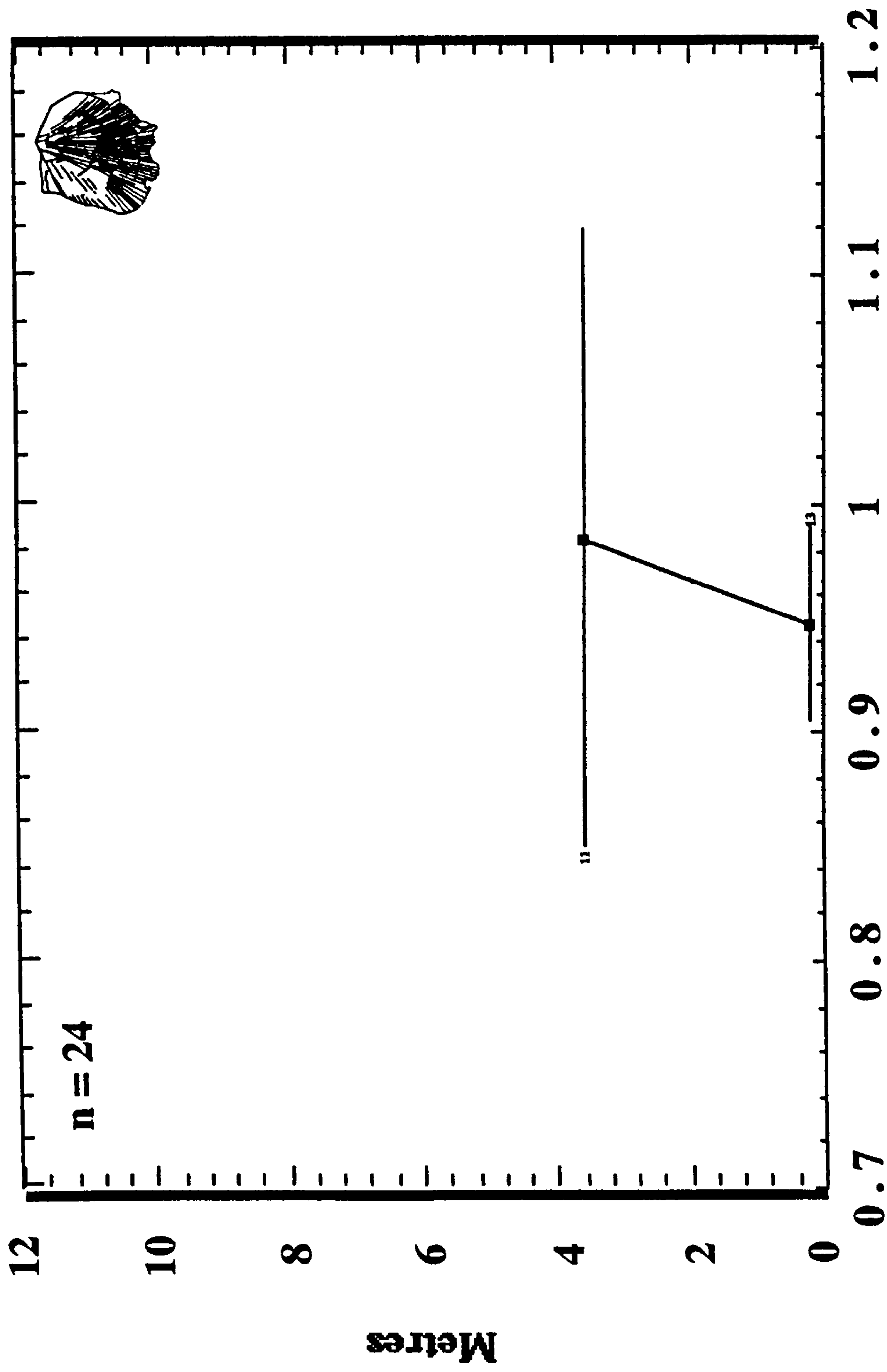


Figure 7.68. 2 individual sample means from the Length to Height ratio for *Meleagrinella braamburiensis*, Orton pit (Figure 7.20).

Error bars represent 95% confidence intervals.

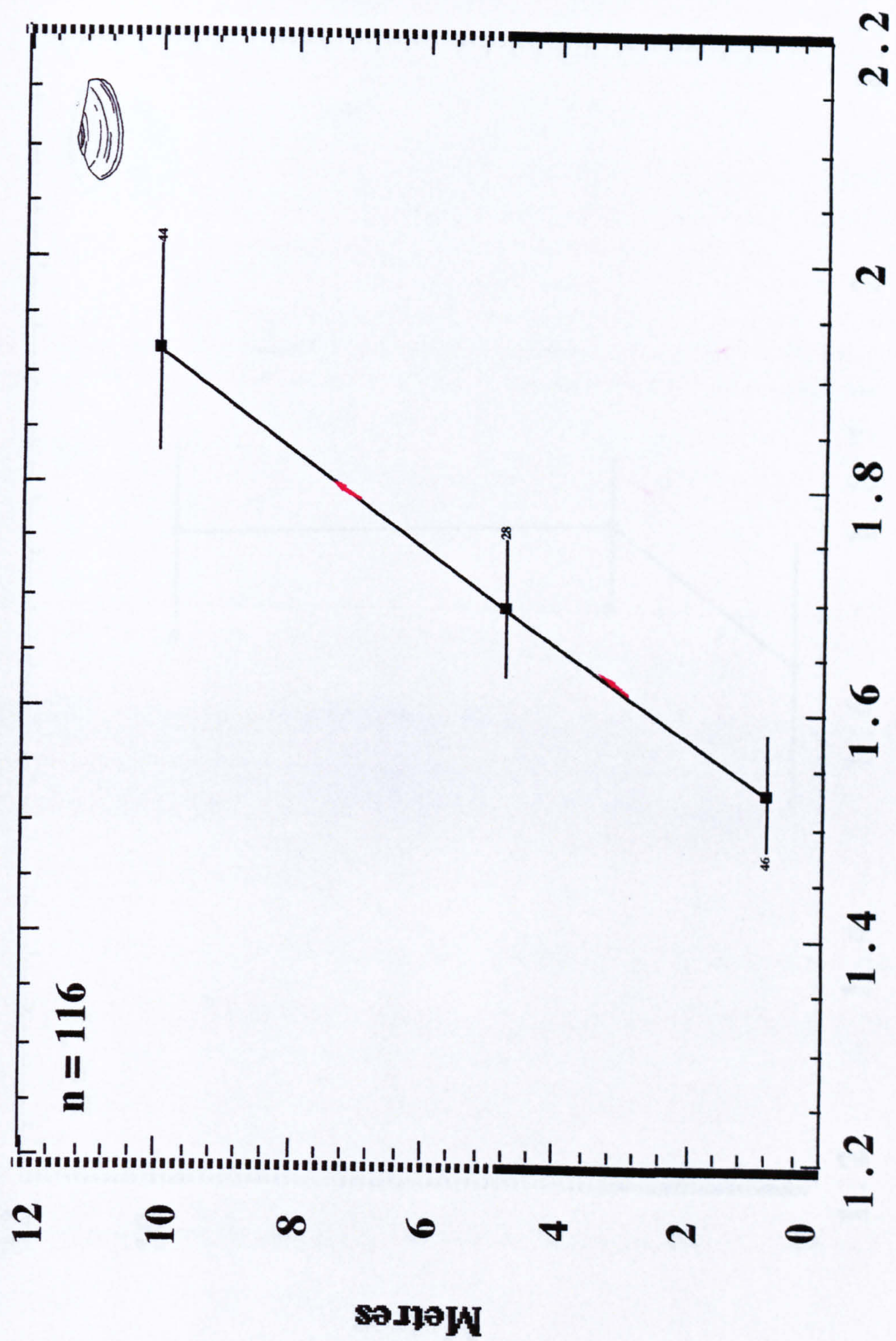


Figure 7.69. 3 individual sample means from the Length to Height ratio for *Mesosaccella morrisi*, Calvert pit (Figure 7.27). Error bars represent 95% confidence intervals.

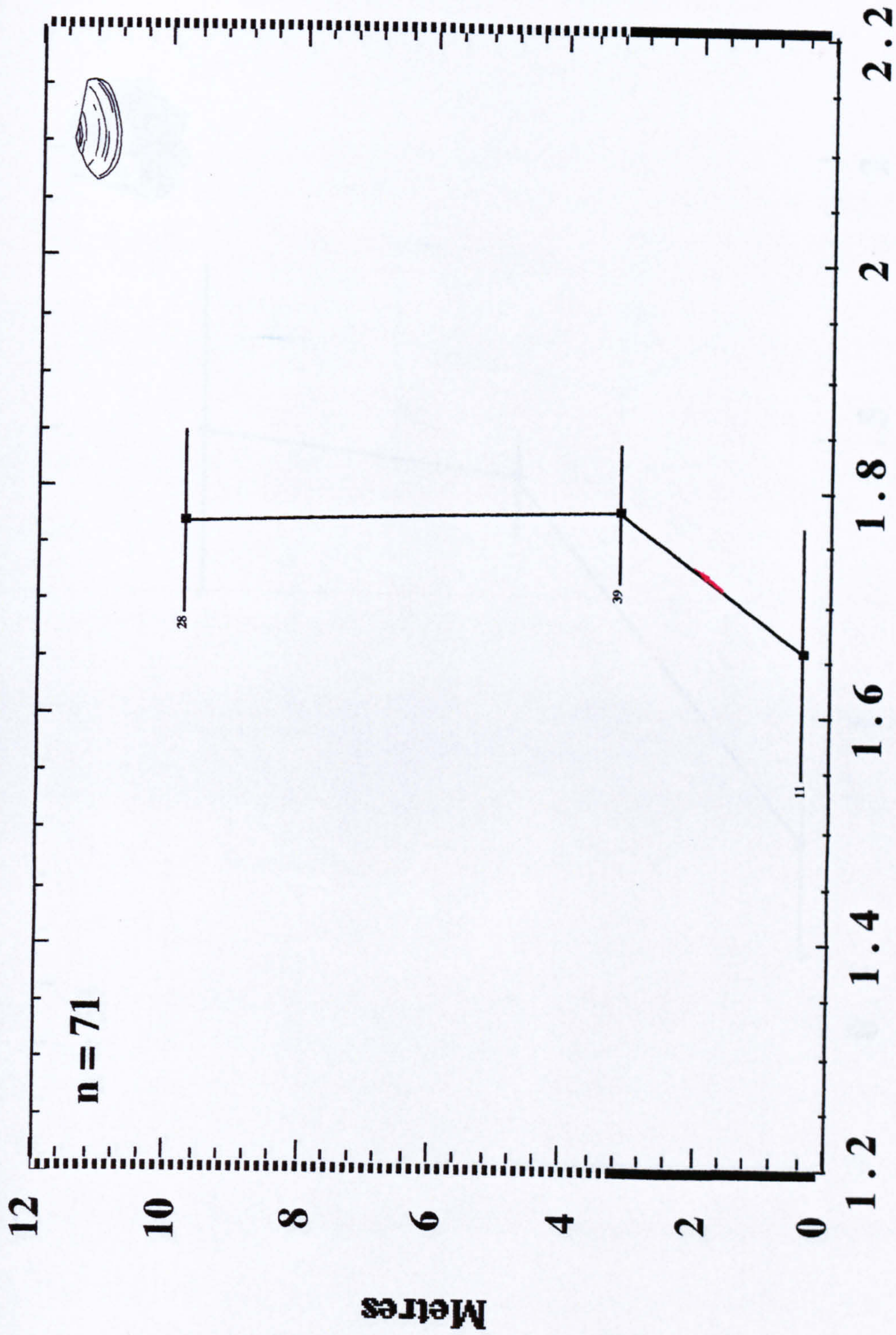


Figure 7.70. 3 individual sample means from the Length to Height ratio for *Mesosaccella morrisi*, Saxon pit (Figure 7.28). Error bars represent 95% confidence intervals.

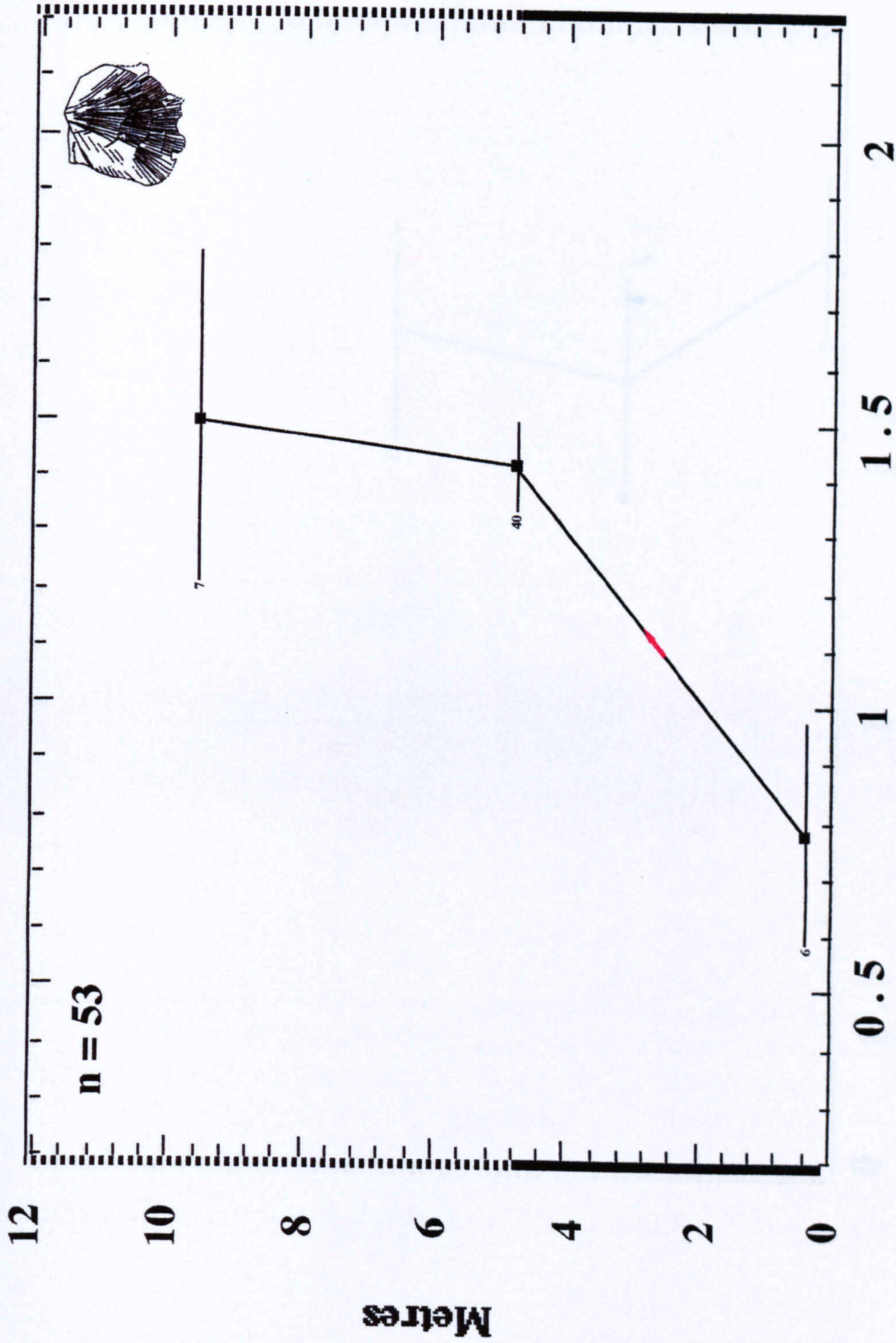


Figure 7.71. 3 individual sample means from the Hinge Length to Anterior Length ratio for *Meleagrinenella braamburiensis*, Calvert pit (Figure 7.33). Error bars represent 95% confidence intervals.

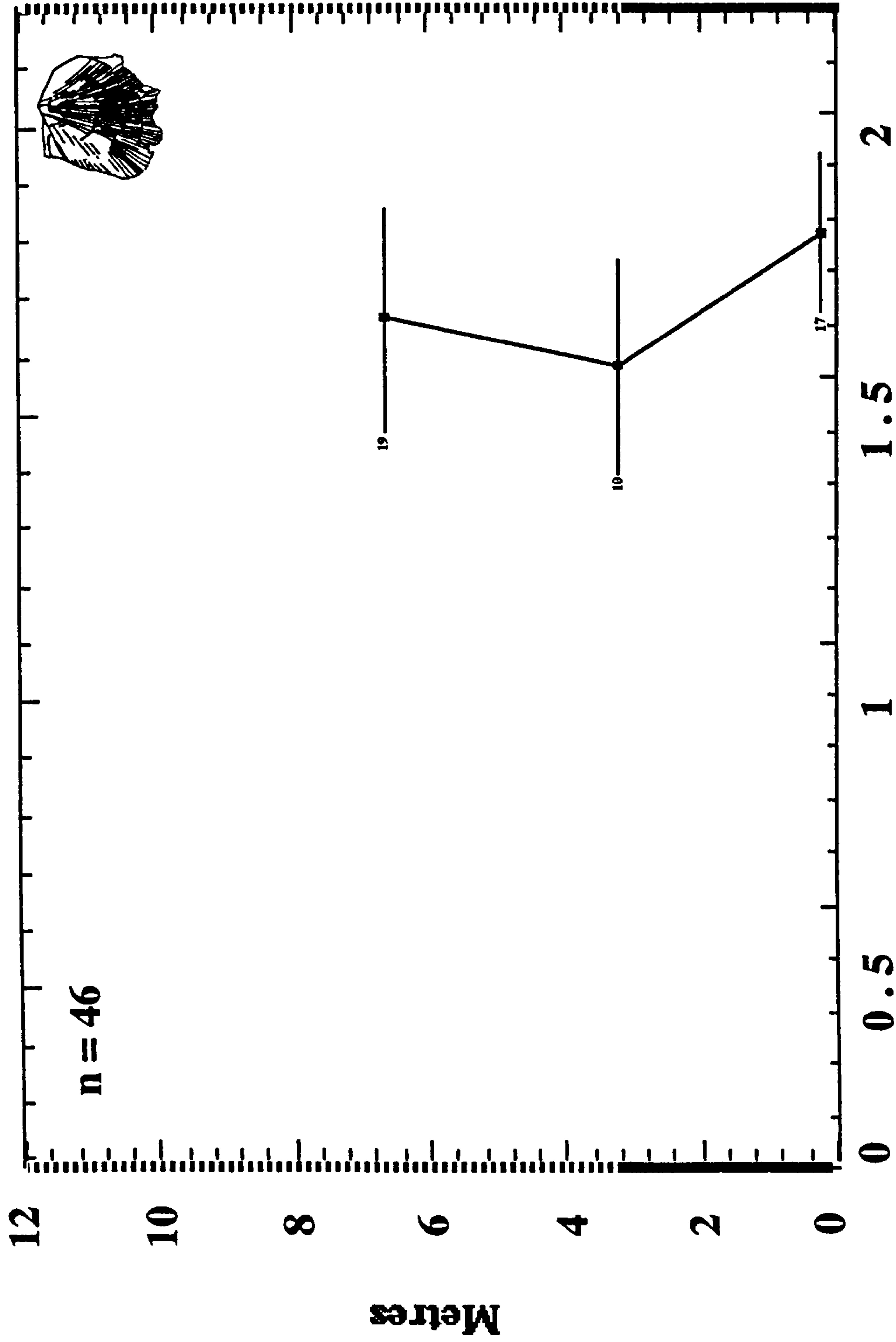


Figure 7.72. 3 individual sample means from the Hinge Length to Anterior Length ratio for *Meleagrinella braamburiensis*, Saxon pit (Figure 7.34).

Error bars represent 95% confidence intervals.

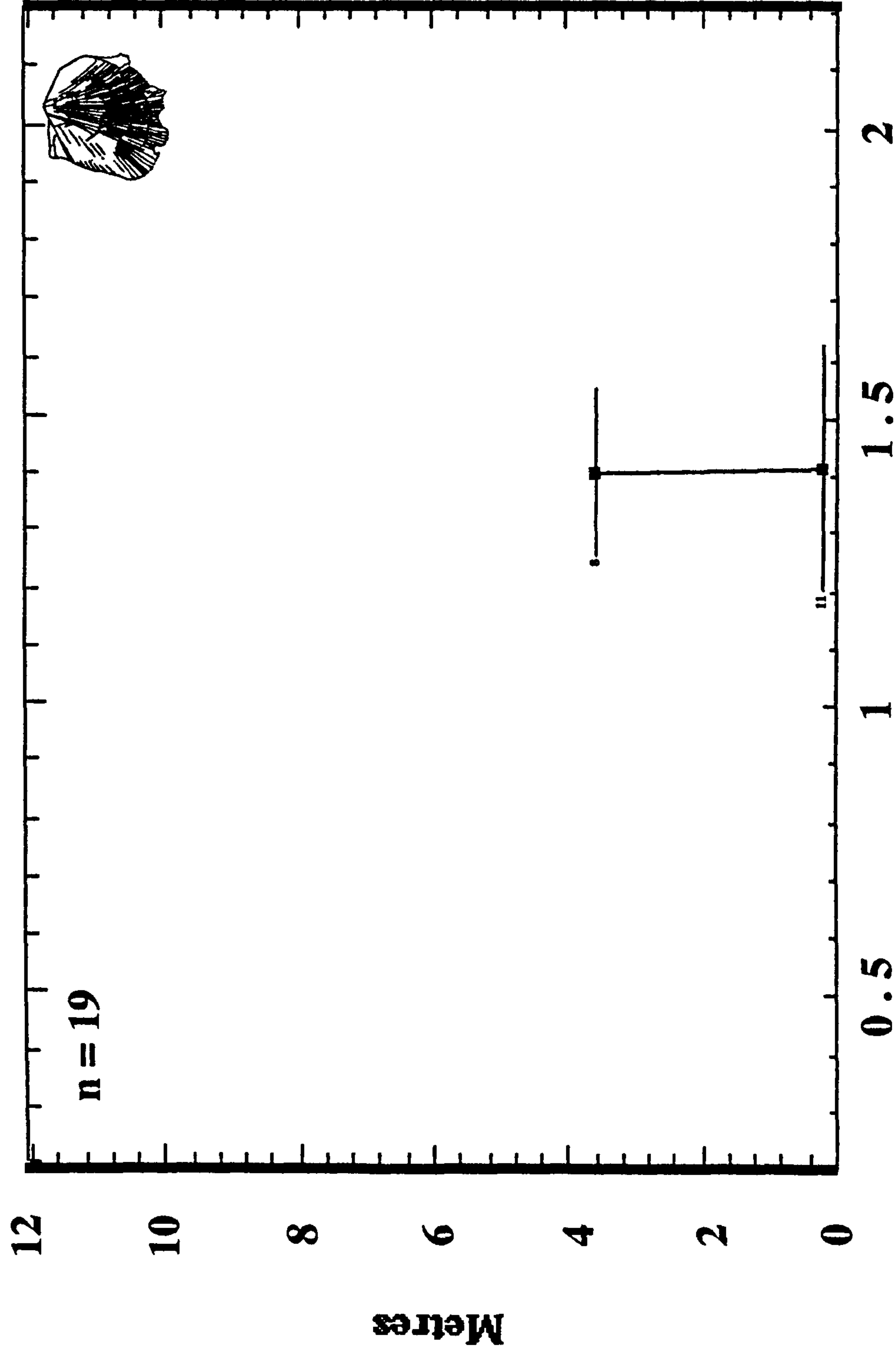


Figure 7.73. 2 individual sample means from the Hinge Length to Anterior Length ratio for *Meleagrinella braamburiensis*, Orton pit (Figure 7.35).
 Error bars represent 95% confidence intervals.

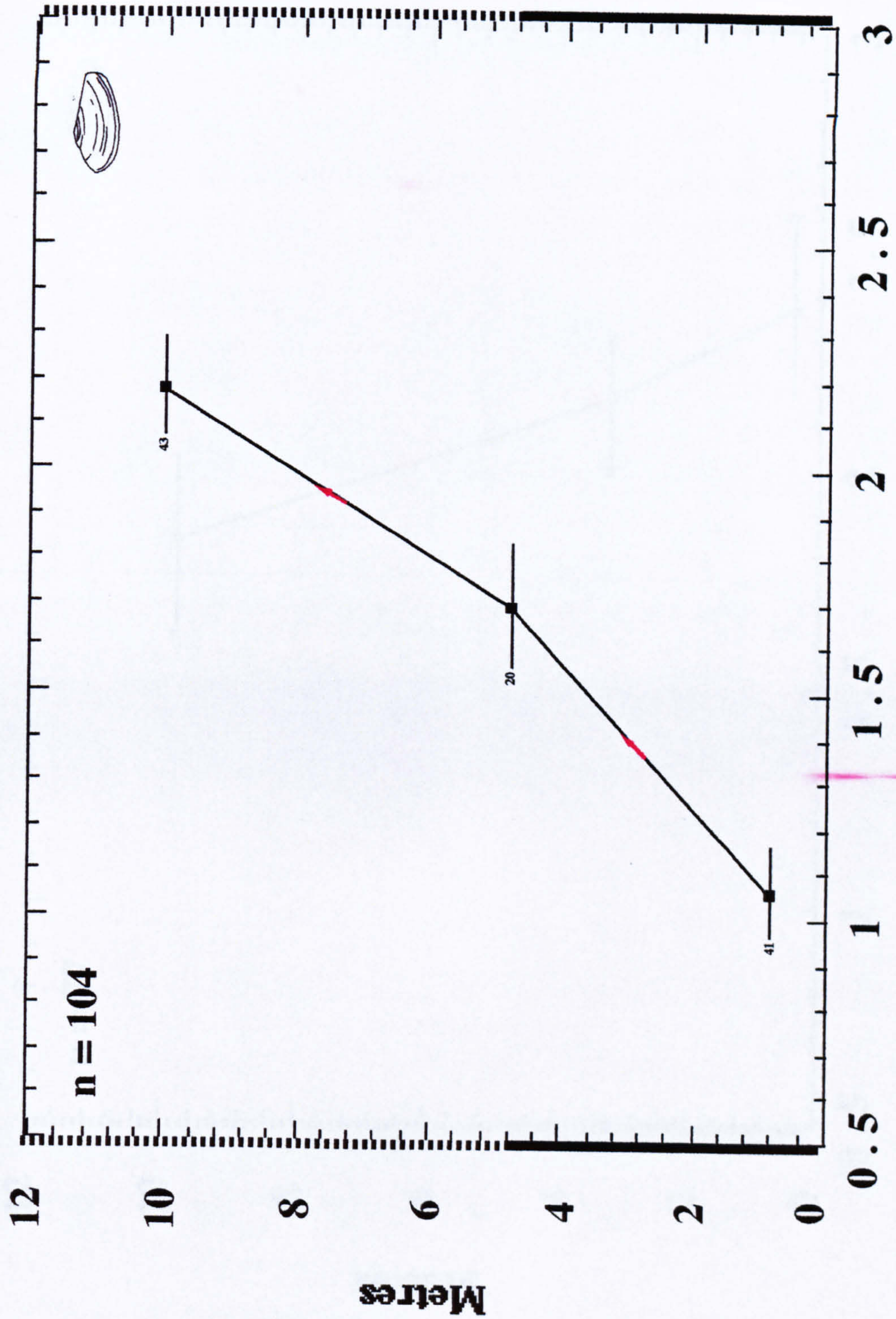


Figure 7.74. 3 individual sample means from the Hinge Length to Anterior Length ratio for *Mesosaccella morrisi*, Calvert pit (Figure 7.42). Error bars represent 95% confidence intervals.

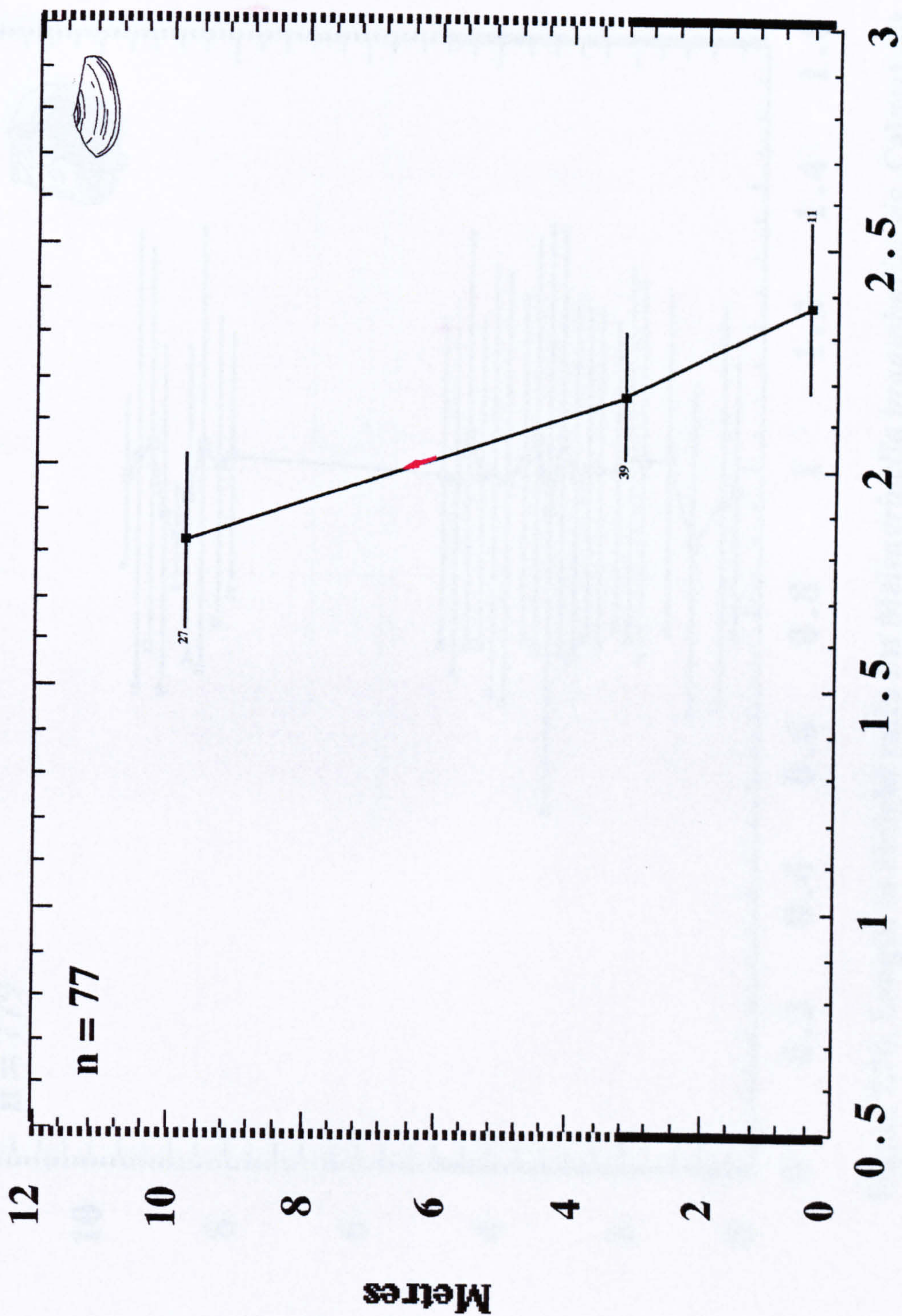


Figure 7.75. 3 individual sample means from the Hinge Length to Anterior Length ratio for *Mesosaccella morrisi*, Saxon pit (Figure 7.43). Error bars represent 95% confidence intervals.

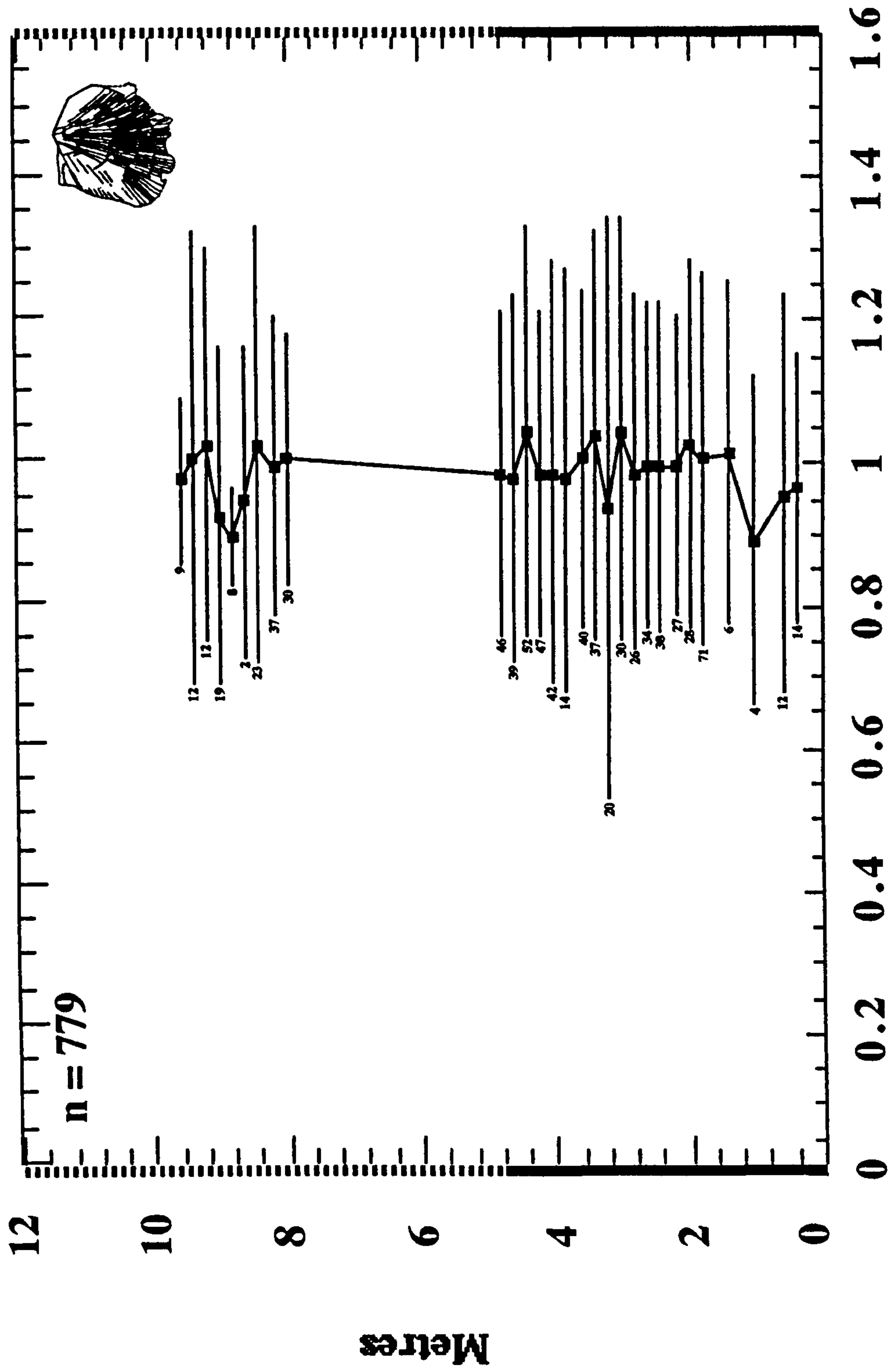


Figure 7.76. Length to Height ratio for *Meleagrinnella braamburiensis*, Calvert pit. Error bars represent 2 standard deviations either side of the sample means; for confidence intervals see Figure 7.18.

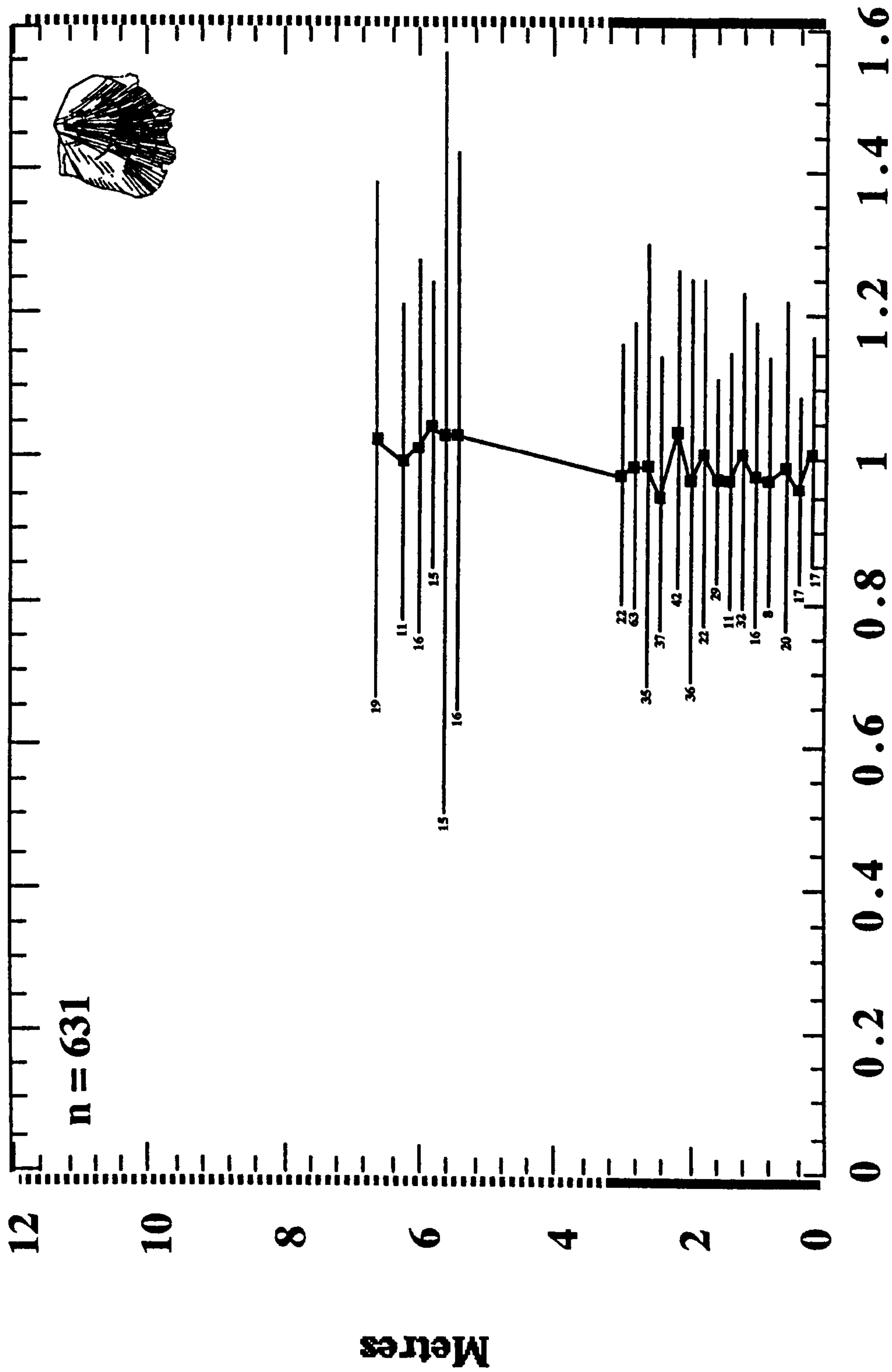


Figure 7.77. Length to Height ratio for *Meleagrionella braamburiensis*, Saxon pit. Error bars represent 2 standard deviations either side of the sample means; for confidence intervals see Figure 7.19.

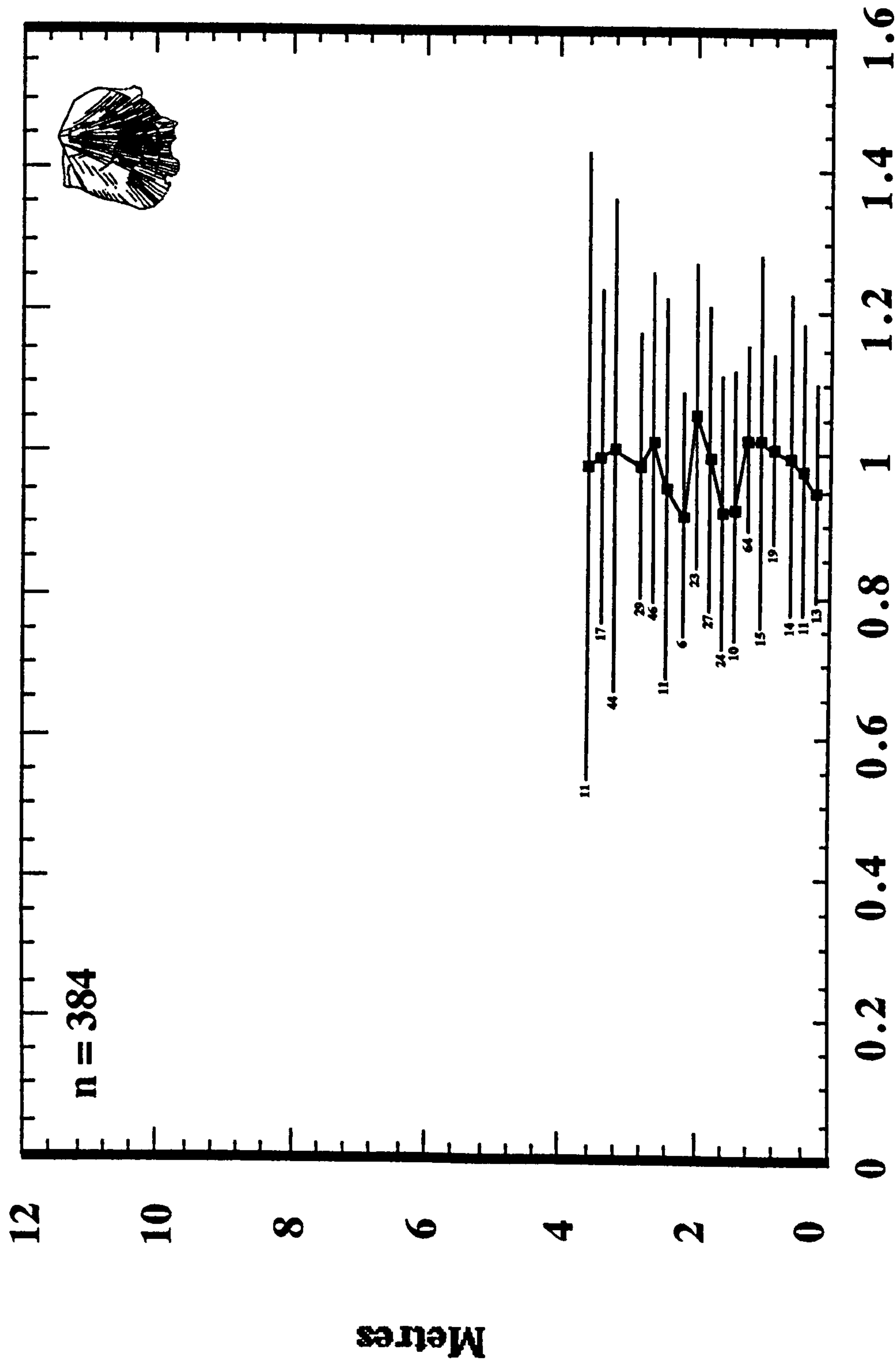


Figure 7.78. Length to Height ratio for *Meleagrinella braamburiensis*, Orton pit. Error bars represent 2 standard deviations either side of the sample means; for confidence intervals see Figure 7.20.

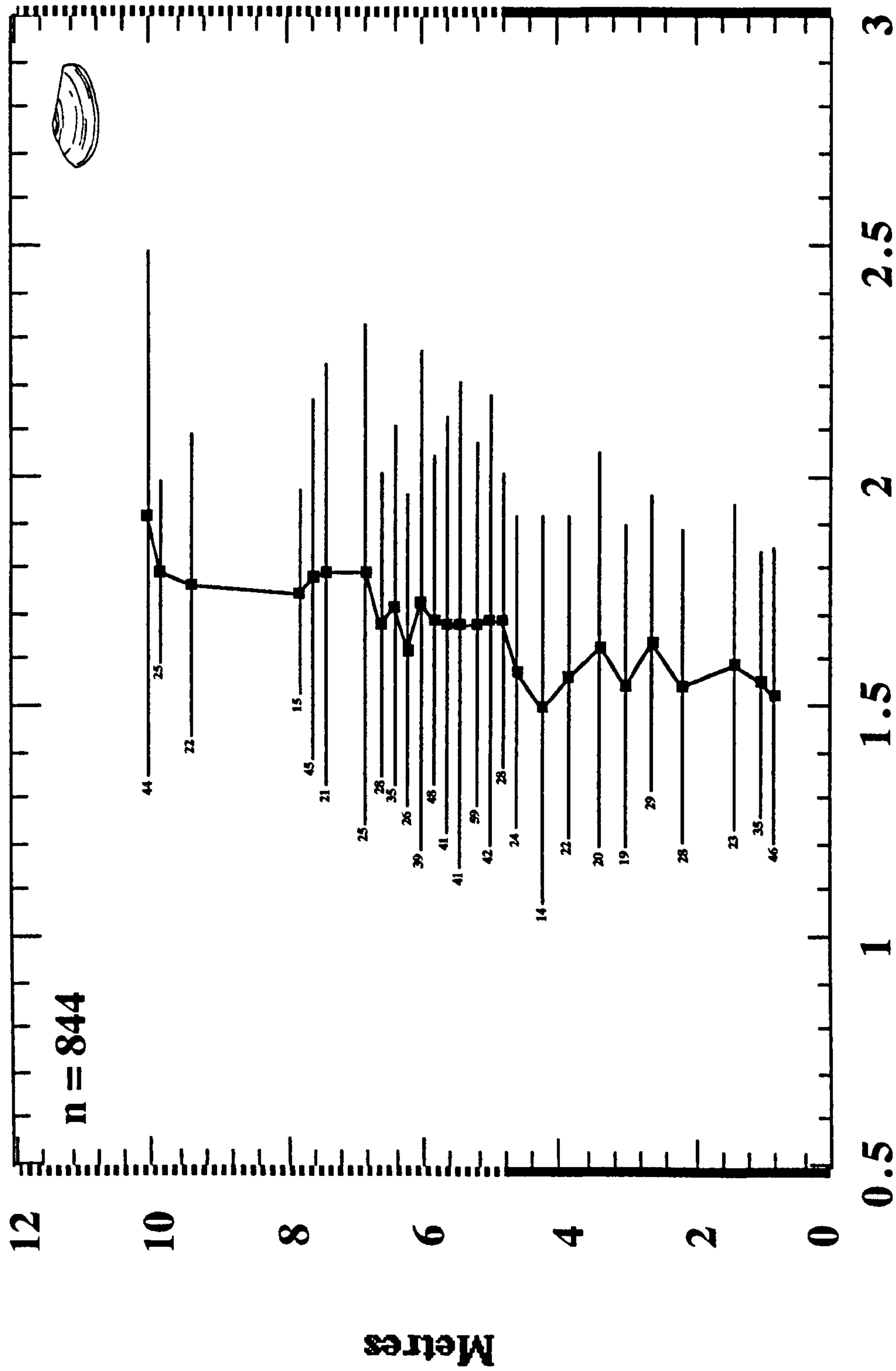


Figure 7.79. Length to Height ratio for *Mesosaccella morrisi*, Calvert pit. Error bars represent 2 standard deviations either side of the sample means; for confidence intervals see Figure 7.27.

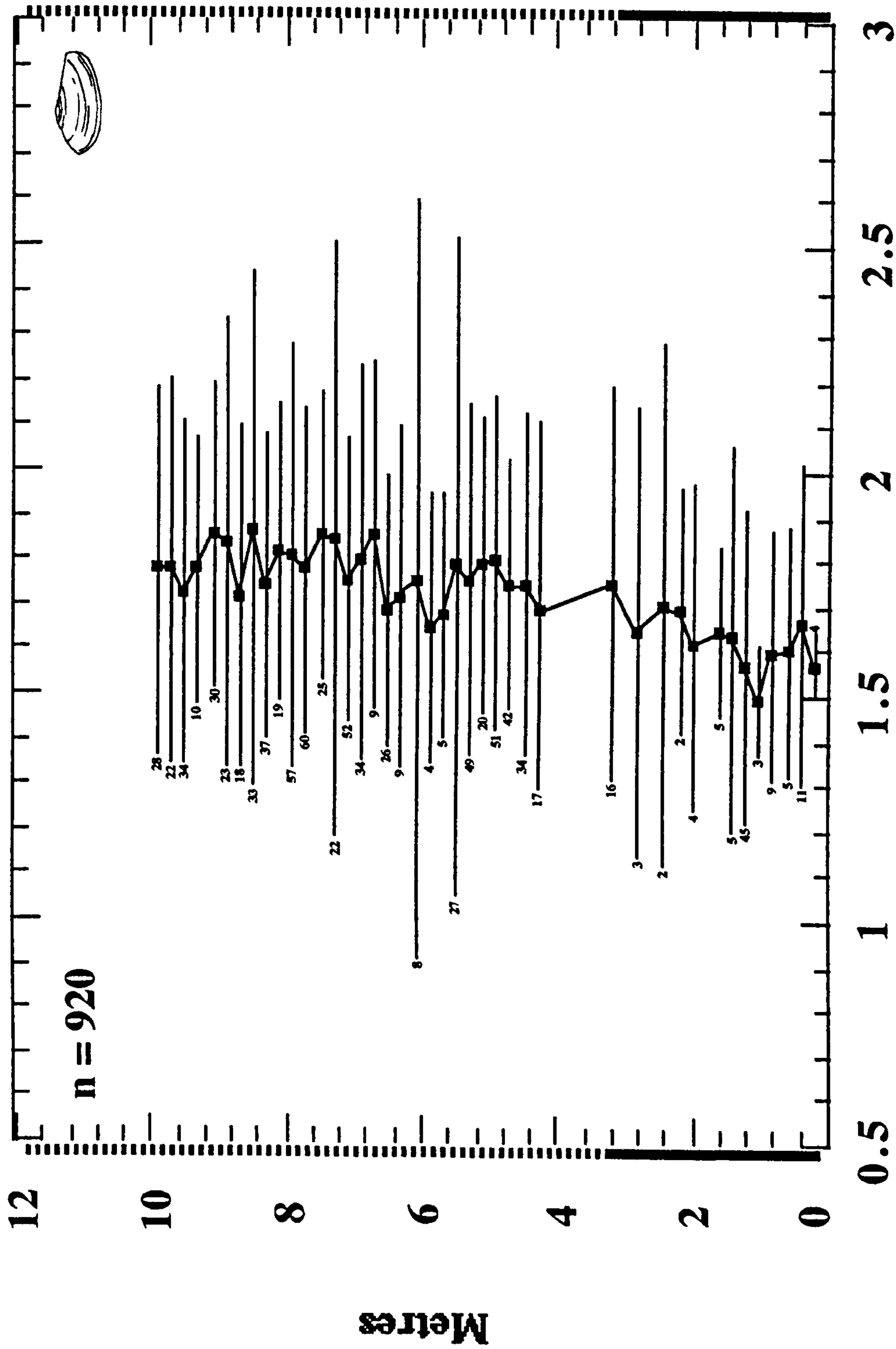


Figure 7.80. Length to Height ratio for *Mesosaccella morrisi*, Saxon pit. Error bars represent 2 standard deviations either side of the sample means; for confidence intervals see Figure 7.28.

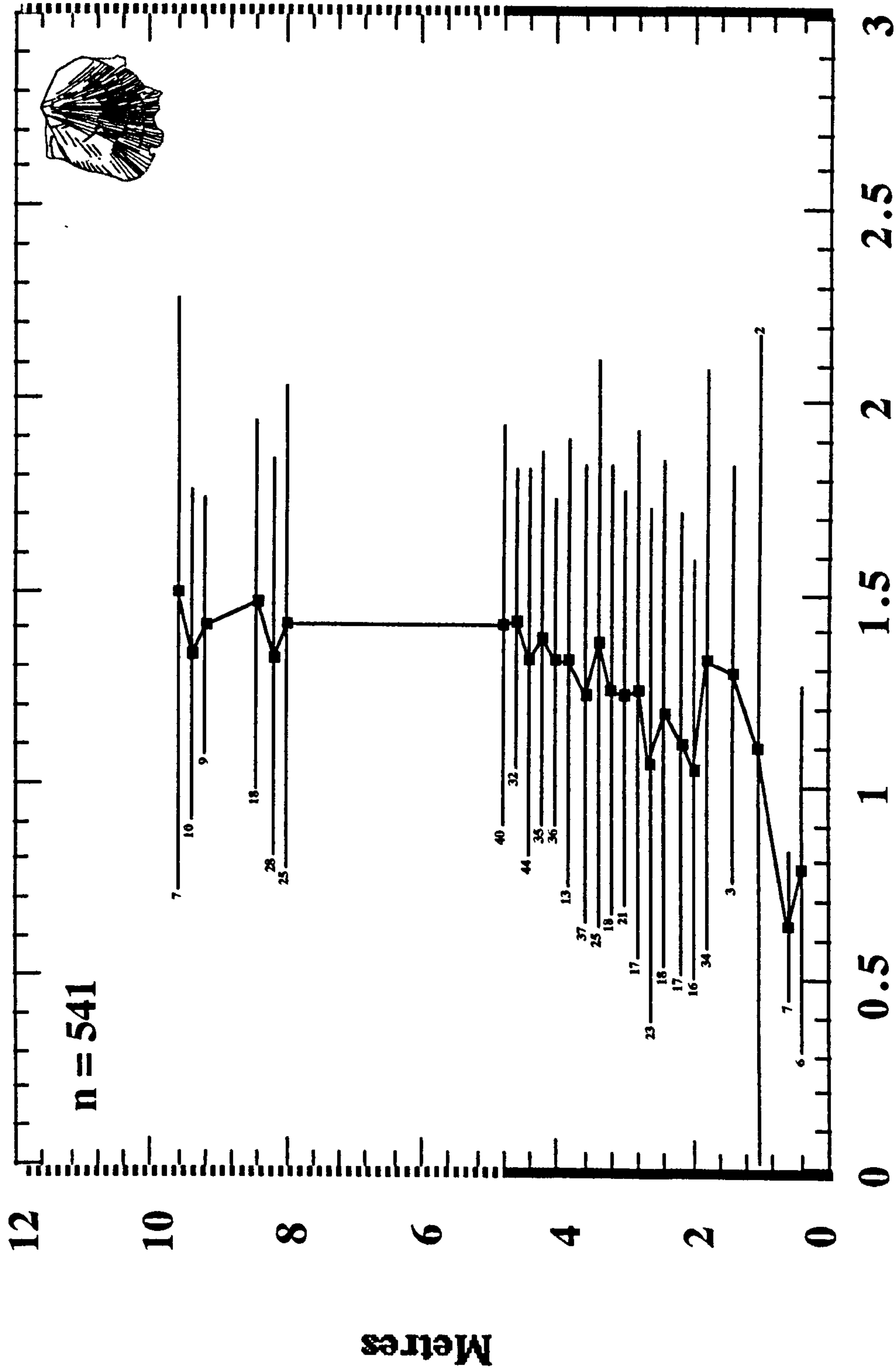


Figure 7.81. Hinge Length to Anterior Length ratio for *Meleagrinnella braamburiensis*, Calvert pit. Error bars represent 2 standard deviations either side of the sample means; for confidence intervals see Figure 7.33

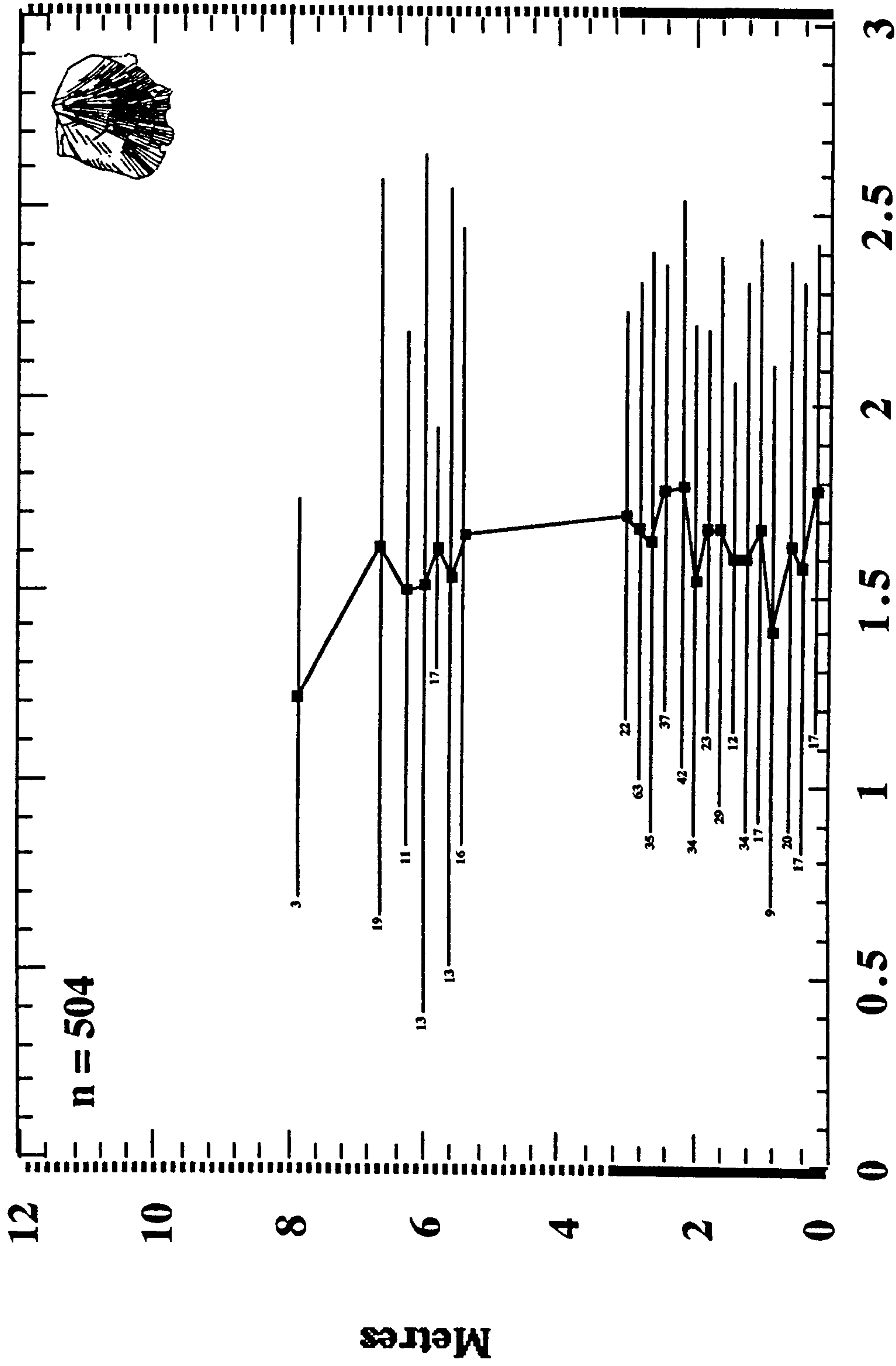


Figure 7.82. Hinge Length to Anterior Length ratio for *Meleagrinnella braamburiensis*, Saxon pit.
 Error bars represent 2 standard deviations either side of the sample means;
 for confidence intervals see Figure 7.34.

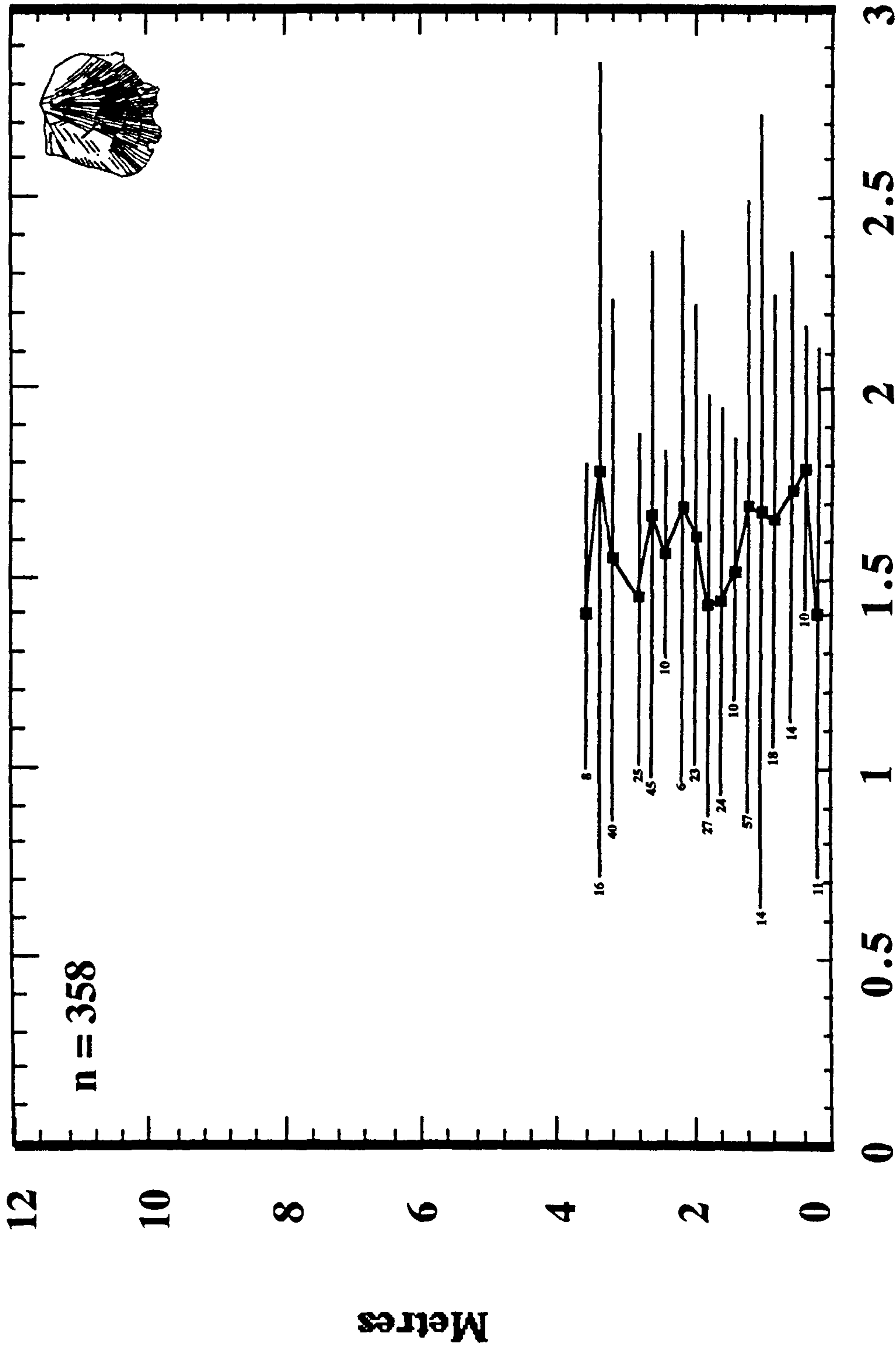


Figure 7.83. Hinge Length to Anterior Length ratio for *Meleagrinenella braamburiensis*, Orton pit. Error bars represent 2 standard deviations either side of the sample means; for confidence intervals see Figure 7.35.

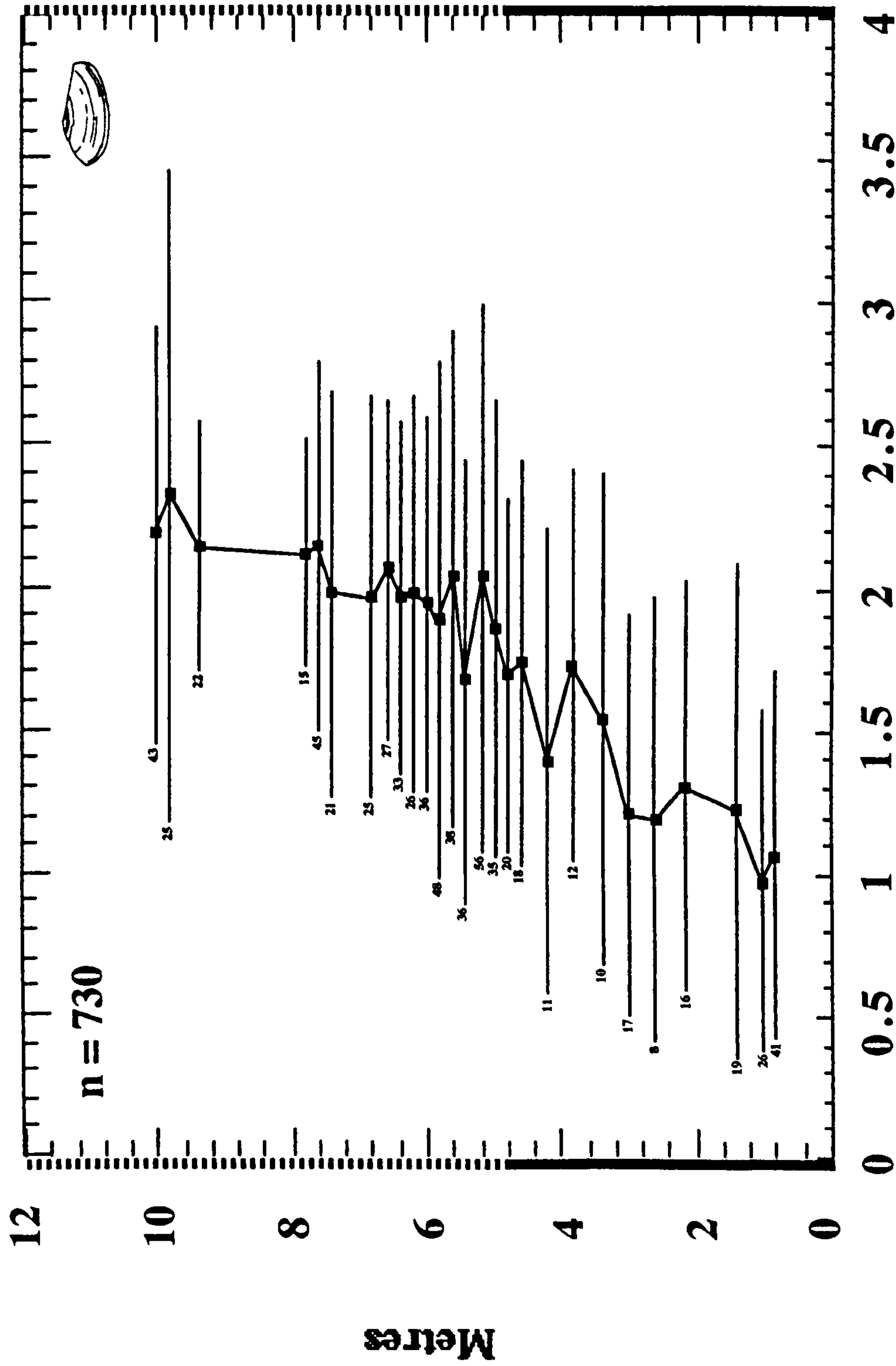


Figure 7.84. Hinge Length to Anterior Length ratio for *Mesosaccella morrisi*, Calvert pit. Error bars represent 2 standard deviations either side of the sample means; for confidence intervals see Figure 7.42.

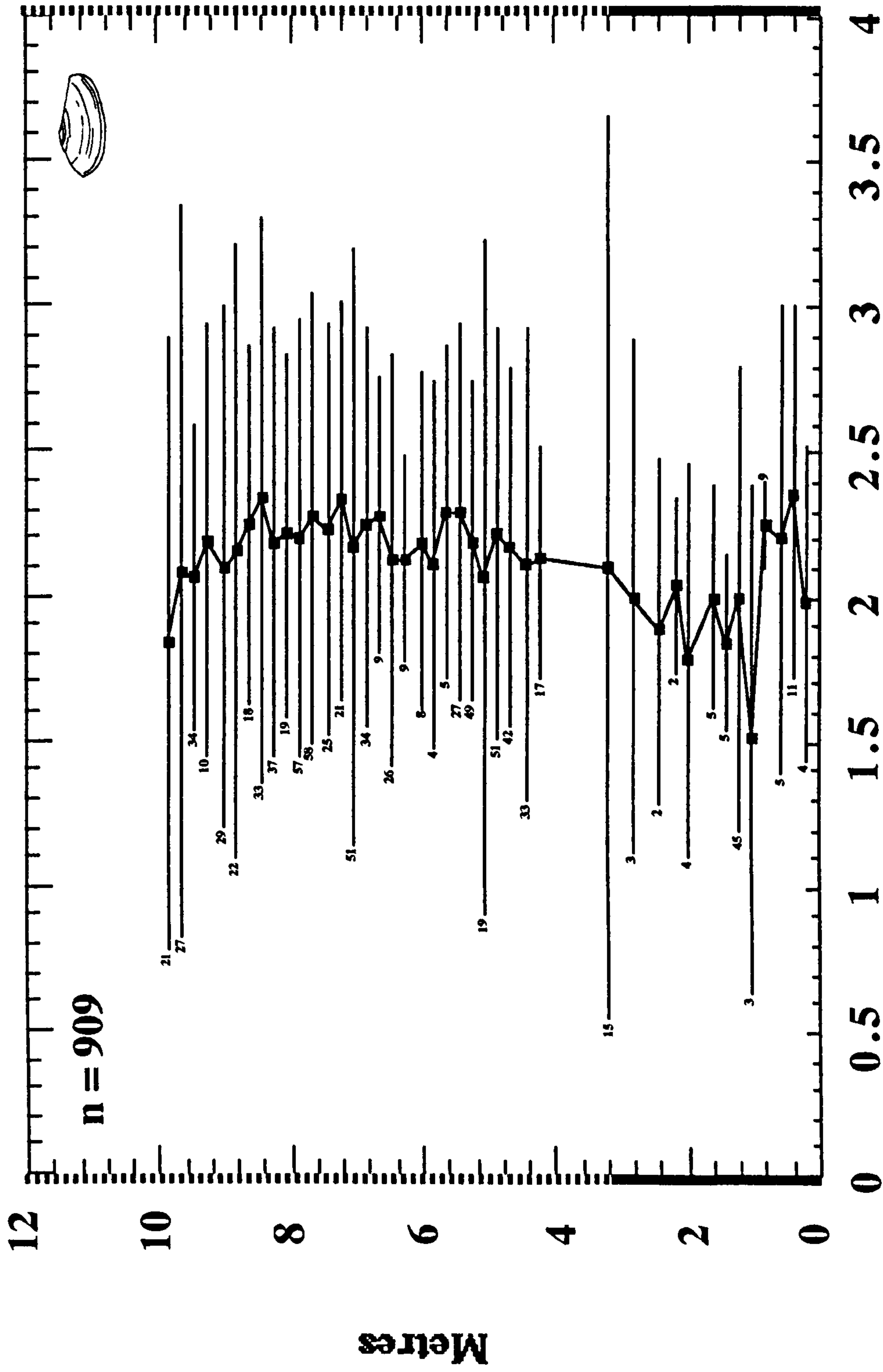


Figure 7.85. Hinge Length to Anterior Length ratio for *Mesosaccella morrisi*, Saxon pit.
 Error bars represent 2 standard deviations either side of the sample means;
 for confidence intervals see Figure 7.43.

VOLUME CONTAINS CLEAR OVERLAYS
OVERLAYS SCANNED SEPERATELY AND
OVER THE RELEVANT PAGE.

Figure 7.86 The Density of Ribs for *M. braamburiensis*, Calvert pit. Black crosses = horizons from the MSZ, red crosses = horizons from the MFZ.

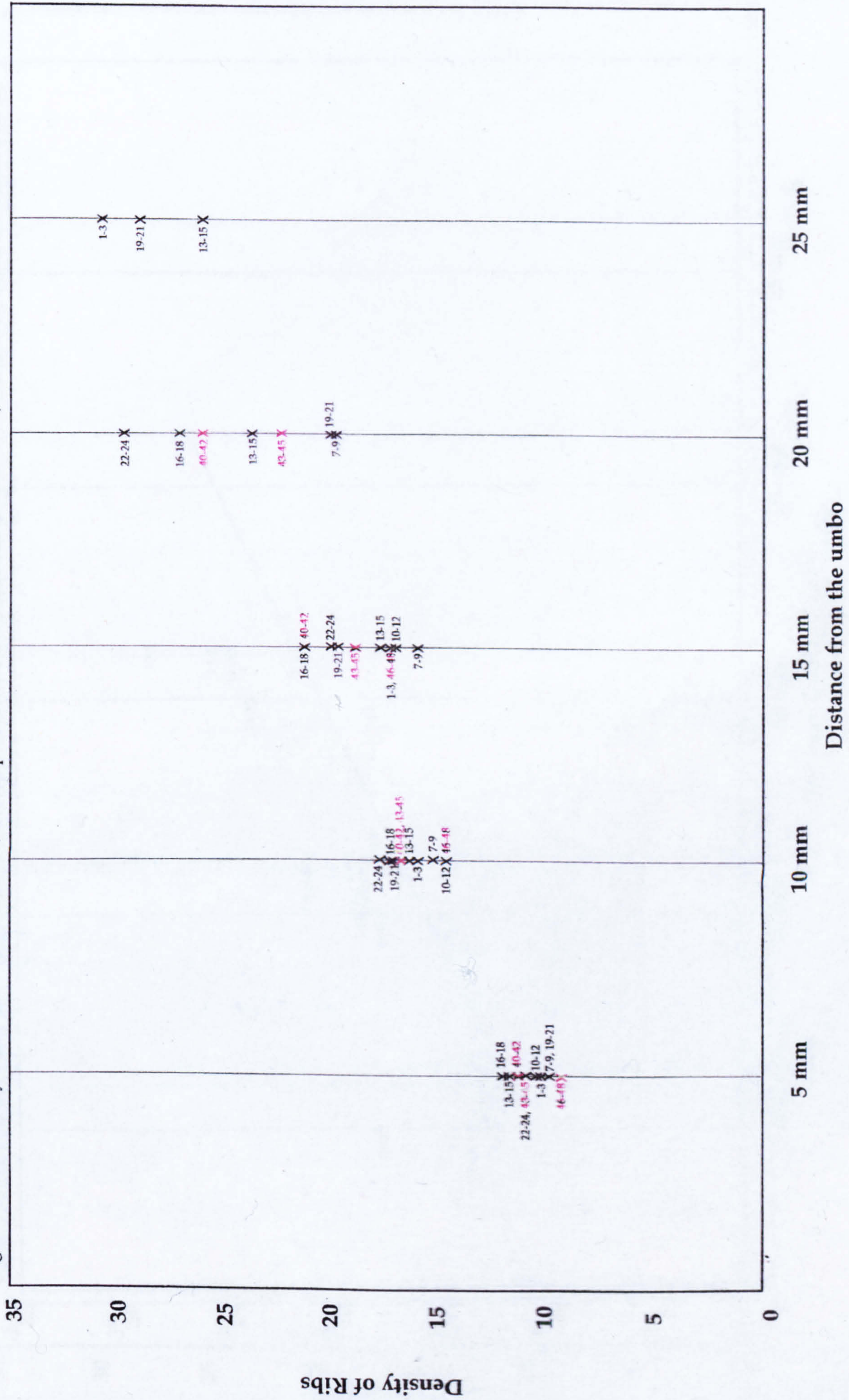


Figure 7.88 The Density of Ribs for *M. braamburienis*, Orton pit. Black crosses = horizons from the MSZ, red crosses = horizons from the MFZ.

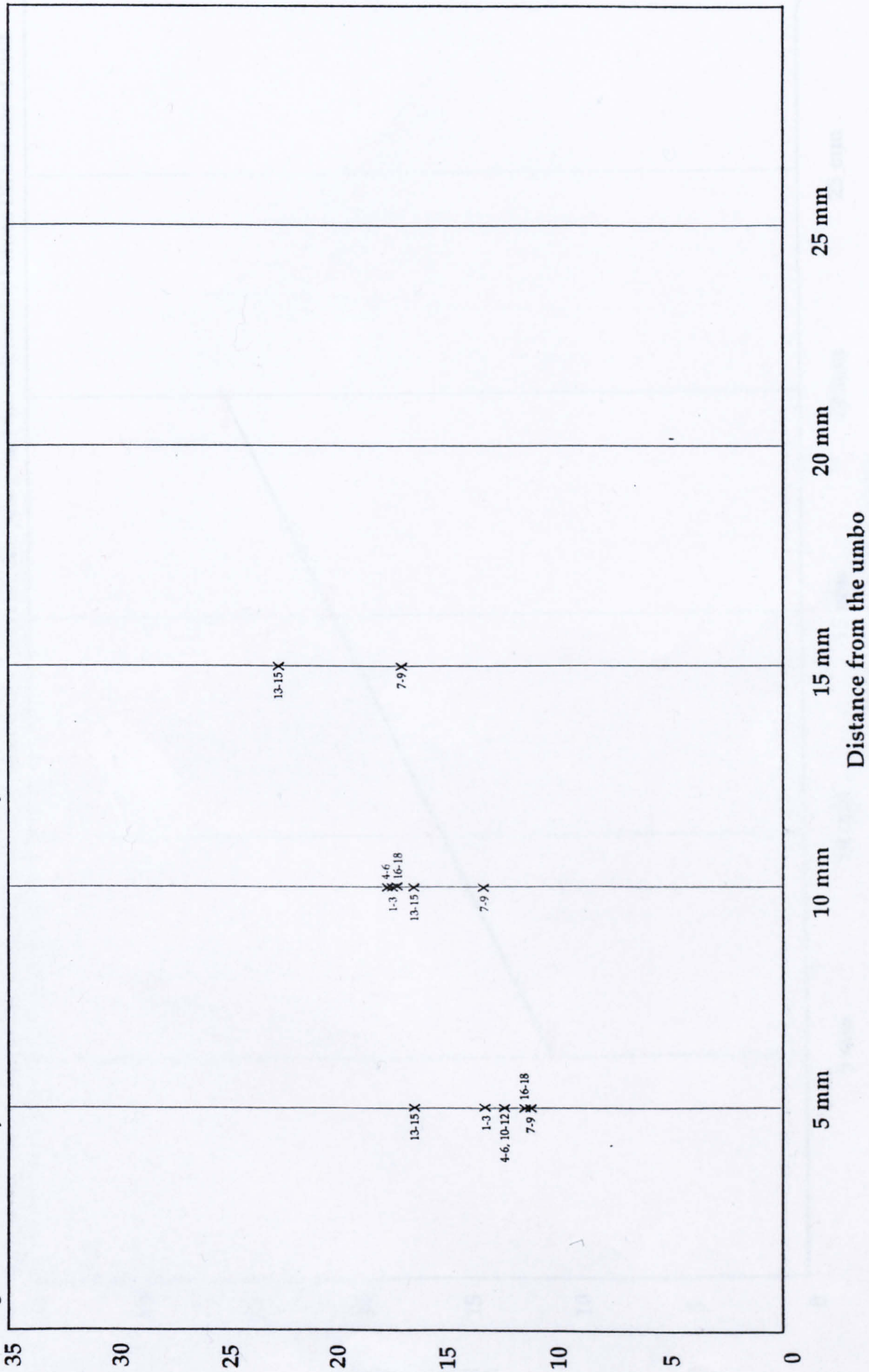


Figure 7.89. The Density of Ribs for horizons 40-42, *M. braamburiensis*, Calvert pit; illustrating the linear relationship between DR and size of shell.

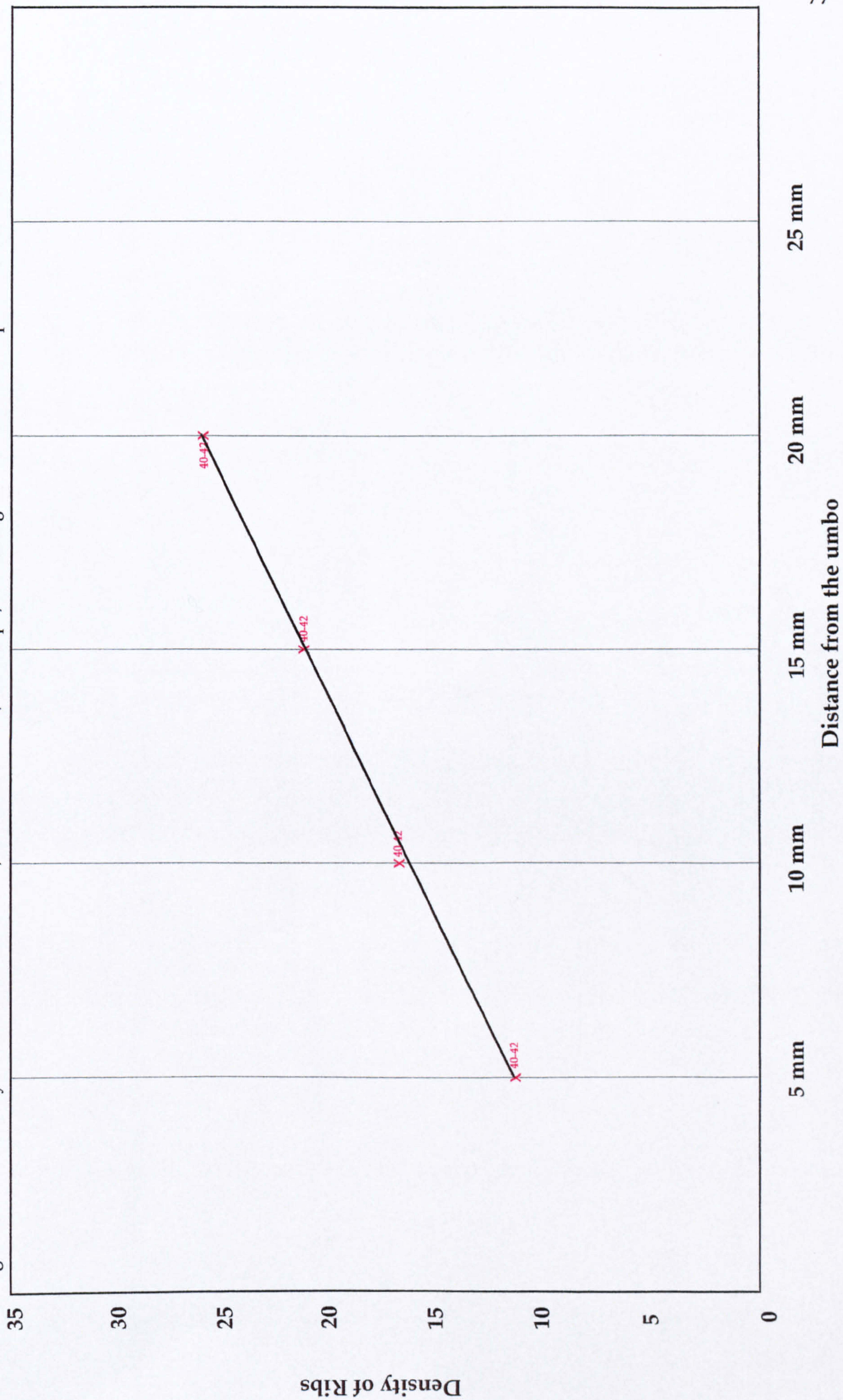


Figure 7.88 The Density of Ribs for *M. braunburienensis*, Orton pit. Black crosses = horizons from the MSZ, red crosses = horizons from the MFZ.

